

INTERSPECIFIC RELATIONSHIPS IN THE POLYPODIUM PECTINATUM-PLUMULA COMPLEX¹

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ABSTRACT

Studies of the life cycle, anatomy, morphology, cytology, ecology, distribution patterns and an analysis of the probable evolutionary relationships of taxa in the *Polypodium pectinatum-plumula* complex, compose the basis of a systematic study of this complex. Field studies in Florida, Jamaica, and Costa Rica, plus use of greenhouse grown plants sent from South America, have aided in the understanding of the biological interrelationships of the taxa. Specimens, including types, from 20 major American and European herbaria have been utilized in this study, which has led to the recognition of 35 taxa, including five new species, three new varieties and six new combinations. Keys, descriptions, typification, synonymy and specimen citations are included for each taxon.

INTRODUCTION

In attempting to understand the interrelationships of the very closely related species of the *Polypodium pectinatum-plumula* complex, studies of the ecology, variation in certain populations, and the natural history of the several species, as well as traditional morphological and anatomical studies, were of considerable help. Because the group has a wide tropical distribution, extensive field studies were not possible, but field studies were made in Florida, Jamaica and Costa Rica, and I obtained living rhizomes of several species for culture from collectors in South America. Although it was necessary to rely heavily on data obtained from the species in Florida and in greenhouse culture, several aspects of the life cycles of these species were examined, and this information was useful in interpreting the remaining species.

Historically, the major preoccupation of taxonomists has been in reducing the enormous and polyphyletic genus *Polypodium* to its present restricted sense. No systematic coverage of this whole group as a unit has ever been attempted, and the taxonomy has consisted mainly of the addition of new taxa one by one. Lindman (1903) treated eight of them in an overall study of tropical American

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species. De la Sota (1960), in his research on the *Polypodiaceae* of Argentina, grouped *Polypodium* into several complexes and treated the eight species of the present group from that country.

MORPHOLOGY AND ECOLOGY

Microscopic morphological observations were facilitated by several techniques. The living material was first killed in FAA (formalin, acetic acid, alcohol) or dried material was relaxed in 5% NaOH for 2-3 days before sectioning. Rhizomes, roots, stipes, and blade segments were sectioned at 25μ on a freezing microtome and mounted unstained in diaphane; or they were imbedded in paraffin, sectioned on a rotary microtome, stained in safranin and fast green, and mounted in diaphane. For studies of venation and epidermal patterns, leaf segments were cleared in 5% NaOH, bleached in 10% Clorox, stained by the tannic acid-ferric chloride method (Foster, 1934) and mounted in diaphane or piccolite. Spore preparations were made either by the acetolysis technique (Erdtman, 1943) and mounted in silicone oil (20,000 viscosity grade), or teased from the frond in 95% EtOH and mounted directly in diaphane.

Gametophytes were grown on a variety of growth media. For young stages, spores were sown on either distilled water or liquid Biejerinck's Solution (Brown, 1920). For later stages and mature gametophytes, spores were sown on agar fortified with Knop's Solution (Brown, loc. cit.) in petri dishes, or sown in 3" porous clay pots with either pulverized sphagnum or hardwood humus. The spores were sterilized by treating them with varying concentrations of Clorox, 10% for 10 minutes being optimal. However, good results were usually obtained in nonsterile conditions. The pots containing soil media were autoclaved, but the petri dishes with agar were not, because it was found that fungi were inhibited when the agar was not autoclaved. Spores, treated either by sterilization or from washed fronds which had been dried in sterilized envelopes, were sown in a sterile transfer chamber.

Gametophytes were observed microscopically either in water mounts, mounted in Hoyer's Solution without being killed, or were killed in 70% EtOH and cleared and stained as the leaf segments above. The small gametophytes were handled in quantity by transferring them in short upright sections of wide glass tubing with the bottom covered with cheese cloth.

Voucher specimens of all experimental collections are deposited in the University of Michigan Herbarium.

RHIZOME

The stem (Fig. 17-19) is a long-creeping to short-creeping or sub-erect rhizome, with the fronds short-spaced (never more than 1.5 cm apart) or approximate to fasciculate and articulate on short pseudopodia 1 to 2 mm long. The plants may be epiphytic, terrestrial, or epipetric, but the rhizomes are always exposed. They vary in diameter from 1 to 3 mm in small species such as *P. truncorum* to 10 to 13 mm in the larger species such as *P. ptilodon* or *P. recurvatum*. The internal anatomy is quite uniform. The vascular system is dictyostelic with 3 (in *P. trun-*

corum) to 17 small exarch bundles in a single ring (Fig. 1, A-C). The endodermis is thin-walled, but the inner wall of the ground parenchyma cells adjacent to the endodermis is always strongly thickened. *Polypodium singeri* and *P. truncorum*, two small epiphytic ferns, show a good deal of dark staining, thick-walled collenchyma tissue in all but the outer portion of the rhizome (Fig. 1, C). No true sclerenchyma tissue is present.

The rhizomes are clothed with paleae throughout, which fall basically into two groups of scales—(a) the most common type, associated with the *P. pectinatum* allies, and (b) those found in the groups of *P. cupreolepis* and *P. truncorum*.

The former group (a) has narrow- to linear-triangular, dark red-brown lustrous paleae, basifixed and with an acuminate or filiform apex. The paleae are either broadly expanded at the basal attachment or have a narrow base at the apex of the rhizome. They are dark colored along their margins, usually with a paler area at the base. The cells are narrow, except at the base of the scale, where they usually become shorter and nearly isodiametric. They are non-clathrate. This is in contrast to several groups in *Polypodium* (such as the *P. vulgare* or the *P. squamatum* groups) in which the paleae are usually basally peltate, at least sub-clathrate, and are usually darker in the center rather than along the margin.

These paleae all have a dorsal cluster of unicellular hairs (and are therefore termed "comose") toward the base of the paleae, which are usually visible under low magnification (Fig. 1, G, J-L). In certain species, such as *P. pectinatiforme*, *P. atrum*, or *P. dispersum*, the hairs are uniformly present, although they may not be conspicuous. In *P. plumula*, on the other hand, the comose hairs are sometimes absent. In *P. bolivianum* the hairs of the paleae are long and dense, and they mostly obscure the scales themselves except at the rhizome apex (Fig. 1, K, L), and in *P. consimile* var. *pastazense* they totally obscure the paleae.

In the second group (b) the paleae are cordate or ovate, basifixed at a single point, not so polished or lustrous as in the previous group, and vary in color from golden to dark red-brown. They are non-comose and either concolorous or sometimes paler toward the base (Fig. 1, I).

ROOTS

The roots are approximately 0.5 mm in diameter with an outer thin-walled cortex of 3-9 layers of parenchyma cells, and a sclerified darkly colored inner cortex usually 4-6 layers deep occupying one-fourth to one-half of the diameter of the root. The endodermis is a thin-walled and inconspicuous layer lining the inner cortex. The bundle is diarch with few (4-8) large tracheids and clusters of small tracheids at the two protoxylem points.

ROOT PROLIFERATIONS

Although root proliferation leading to sporophytic reproduction is known in pteridophytes, it is infrequent. Root proliferations are known in *Platyserium*, *Amphoradenium* (syn. *Adenophorus*), and *Asplenium*, and in the present study they have been found to occur in *Polypodium dispersum*, *P. ferrugineum*, *P. filicula*, *P. pectinatum*, *P. plumula*, *P. siccum*, and *P. singeri* (Fig. 7).

Although root proliferations have occasionally been thought to be new plants arising from slender elongated stems or rhizomes (similar to the stolons of *Nephrolepis*), this is not the case in the present complex. As seen in cross-section, a single vascular trace of the root type crosses the cortex of the parent root. The new rhizome is usually first noticed as a small scaly bump approximately 1 mm in diameter on the side of the root. New roots and leaves develop in typical fashion from this small rhizome.

JUVENILE LEAVES

Within the *Polypodium pectinatum-plumula* complex, sporophyte leaves of a "juvenile type" can develop from any of three sources—from root proliferations in various species (as discussed above), from apogamous outgrowths in *P. dispersum* and from sexual embryos.

Leaves produced from root proliferations and from gametophytes have the same morphological stages. Figure 2, D-F, shows the developmental leaf series of *P. dispersum*, *P. plumula*, and *P. ptilodon* var. *caespitosum*. The first leaves are invariably simple and elliptic with a single midvein of spirally thickened tracheids. The first leaves of *P. ptilodon* var. *caespitosum* are larger and more broadly elliptic than those of either *P. dispersum* or *P. plumula*. The three hair types, discussed below, appear on the first leaves of all the species listed (Fig. 15, C, D, F, G), except that ctenoid hairs are lacking on *P. plumula*. After the second or third leaf, the veins become forked and the blade becomes lobed. The leaves which follow are alternately lobed. Subsequent to these are leaves which are sub-oppositely lobed as in the mature leaf. The venation then develops the mature condition of being 2 or 3 times forked (Fig. 2). No young stages of any of the species with anastomosing venation were available for study, but presumably they follow the same pattern modified only by vein fusions.

MATURE LEAVES

The fronds may be upright, curved or pendent. Most of the species have upright and rather stiff fronds, but certain of the epiphytic ones with upright rhizomes attached to vertical substrates tend to have more flexuous or pendent fronds, such as *P. plumula* (Fig. 3, F), *P. curvans* (Fig. 3, C), *P. choquetangense*, *P. siccum*, or *P. truncorum*.

The frond outline is narrow-elliptic, -ovate, or -deltoid (Fig. 3). In those species that have narrowly elliptic fronds (e.g. *P. plumula*, *P. alfredii*, or *P. cupreolepis*) and those with narrow-ovate fronds (e.g., *P. ptilodon*, *P. dispersum*, *P. atrum*, or *P. camptophyllum*) the stipe may be long or short. Several of the species have the lower segments contracted quite abruptly, as in *P. plumula* (Fig. 3, F), and a long stipe; in others, such as *P. consimile* or *P. filicula*, the stipe is reduced or almost absent, and the basal segments are very gradually reduced to lobes. The deltoid or subdeltoid fronds, such as those of *P. recurvatum* (Fig. 3, G) and *P. bolivianum*, have an abrupt demarcation between stipe and rachis at the base of the blade.

The fronds are articulate, abscissing from a short pseudopodium. The tip of

the frond and the segments curl tightly adaxially in response to drought, either from atmospheric dryness or water loss after collection. The whole group possesses the ability to respond in this manner, but it is most strongly expressed in such species as *P. plumula*, *P. dispersum*, *P. filicula*, and *P. cupreolepis*. Both this curling ability and the articulation of the fronds reduce the exposed leaf surface, and appear to be adaptations to the epiphytic or epipetric mode of life and to periods or seasons of little atmospheric humidity.

STIPE AND RACHIS

The stipe and rachis are distinctive. In the mature leaf the main axes are either black or of various shades of red-brown; they always have a highly polished appearance. In juvenile fronds the main axis may be lighter or even stramineous, but it turns dark and lustrous as the blade matures. The only exception is that certain of the northern plants of *P. hygrometricum* have a light axis even at maturity, although the majority of specimens of this species have dark axes. The color may also vary between living and dried plants. The axes of *P. dispersum* and *P. plumula* are black in both states. In *P. recurvatum*, *P. truncorum*, and *P. ptilodon* var. *ptilodon* they are red-brown in both the living and dried state. *Polypodium ptilodon* var. *caespitosum* has a consistently red-brown axis and costa when dry, but the axis is quite blackish in living material. A wide sclerified layer in the outer cortex gives the axis its hard and lustrous external appearance. This layer also gives the rachis the characteristic springiness or elasticity readily recognizable even on herbarium sheets, particularly in the strongly pendent epiphytes, such as *P. plumula*. In *P. curvans* and *P. choquetangense* the main axis is usually sinuous or contorted, and the apex of mature fronds often remains circinate.

The stipe and rachis are terete, and the stipe has either narrow wings or narrow lateral green stripes along its entire length.

TRICHOMES

Three types of hairs are present on the fronds of these ferns, as illustrated in Fig. 4. (1) The first is a small, simple, clavate hair composed usually of only two or three cells, the terminal one being somewhat larger and blunt-tipped (Fig. 4, I₃). These hairs are usually no longer than 150 μ . (2) The second type is apparently derived from the first. In its most characteristic form, this hair consists of an arched axis of approximately four cells, with lateral branches usually of only one, sometimes two, cells. There are usually three or four of these lateral branches all arising from one side producing a "ctenoid" hair. However, modifications of this type of hair are frequent in which the number of branches is reduced, sometimes to one, thus suggesting intergradation with the simple clavate hair (Fig. 4, I). (3) The third hair type is a long, simple, acicular, multicellular hair (Fig. 4, J₃, K₄). These hairs are usually pale on the young frond and turn a golden color at maturity. The acicular hairs vary considerably in length, from 0.2 to 2.0 mm. They are of diagnostic importance in several species, as indicated below.

The three hair types are found on the stipe, rachis, costa, and lamina. The ctenoid hair is apparently present on all juvenile fronds, but is not present on the

mature fronds of *P. plumula*, *P. cupreolepis*, *P. truncorum* and their immediate allies. The small, clavate hairs are universally present, primarily on the lamina. They are usually so short as to be overlooked, except in *P. sursumcurrens*, in which they are long, blackish, and visible to the naked eye. The acicular hairs have not only considerable variation in size, but vary also in density and distribution. They are absent in a few species, such as *P. bolivianum*, and are only scattered on the lamina in most species, but are quite abundant and dense in *P. pectinatum*, and *P. camptophyllum*. In all four varieties of *P. ptilodon* the acicular hairs have a curious pattern of distribution such that the lamina is essentially glabrous except for an oval area of dense pilosity around the sorus, often visible to the naked eye or with a hand lens (Fig. 1, E). These are not to be confused with the receptacular paraphyses discussed below.

PALEAE

The most frequent type of rachis scales or paleae are those of the *P. pectinatum* allies (Fig. 5, H, K) which are long, filiform, inconspicuous, and few in number. They are uniformly dark red-brown and of long, thin cells, except that they have more lightly colored and small isodiametric cells at the base. They occur on both the upper and lower surfaces of the main axis, although usually only on the stipe and lower portion of the rachis. At the base of the stipe they tend to have broader bases and approach the shape of the rhizome paleae, which, in the *P. pectinatum* assemblage, are invariably linear-triangular. The margins are entire except in *P. bolivianum*, where they have simple or forked fimbriae on the margin, and in *P. eurybasis*, which occasionally shows slightly fimbriate margins. In both of the latter species this is an amplified condition as regards stipe paleae, and approaches the more fimbriate condition of the rhizome paleae of those species. Several other species, such as *P. pectinatum* or *P. camptophyllum*, have inconspicuously fimbriate rhizome paleae, but have entire rachis paleae. This is thus apparently a relative change: those species with quite heavily fimbriate rhizome paleae show some indication of this on the rachis paleae, but those species with few or no fimbriae on the rhizome paleae lack any at all on the paleae of the rachis.

The second group of species (*P. atrum*, *P. dispersum*, *P. bermudianum*, *P. plumula*, *P. filicula*, *P. ferrugineum*, *P. cupreolepis*, *P. alfredii* and *P. sursumcurrens*) have rachis paleae which are non-filiform (Fig. 5). They may be narrow-elliptic (*P. alfredii*, *P. sursumcurrens* and *P. ferrugineum*) (Fig. 5, F), narrow-triangular with irregular hastate bases (*P. dispersum*, *P. atrum*, *P. bermudianum*, and, in part, *P. plumula*) (Fig. 5, A₄₋₇, B, C, D, J) or they may be essentially cordate, as in *P. plumula*, *P. filicula*, and *P. cupreolepis* (Fig. 5, A₁₋₃, G, I, L). In all but the narrow-elliptic paleae, the margins may be inconspicuously and irregularly fimbriate (Fig. 5). *Polypodium filicula* is the only species with cordate or triangular paleae in which most paleae have an entire margin. Except for overall shape, all of the paleae of this group of species are similar to those of the rhizome in coloration and cell structure. Those species with hard, lustrous, red-brown rhizome paleae have similar rachis paleae. Species such as *P. cupreolepis* (Fig. 1, I and Fig. 5, G) and *P. ferrugineum*, with pale and dull rhizome paleae, have similar rachis paleae.

The narrow-elliptic paleae on the rachis are sparse like the filiform paleae in the previous group. However, those species with hastate-triangular or cordate paleae possess them on the rachis in greater quantity, so that they are readily visible to the unaided eye.

In all taxa except *P. plumula* and *P. filicula* the paleae are flat at the base. In the two exceptions the scales appear inflated or "bullate" at the base. This character appears occasionally also in the paleae of *P. curpreolepis*.

The species with conspicuous and numerous rachis paleae (*P. atrum*, *P. bermudianum*, *P. dispersum*, *P. plumula*, *P. filicula*, and *P. cupreolepis*) also have paleae on the costae. In all cases, these are reduced paleae similar to those of the rachis. In some, as shown in *P. plumula* (Fig. 4, H), the homologies between paleae and hairs are apparent. Although there are basically only three hair types, as described above, in those taxa with costal paleae an additional large, many celled, clavate, simple hair is also present. It is evident that this is the ultimate reduction of the paleae.

SEGMENTS

Figure 6 illustrates outlines and venation patterns of the segments of representative species. Figure 3 shows the orientation of the segments in selected species. All the species have simple and entire segments except *P. eurybasis*, *P. curvans* and *P. paradiseae*, which have crenate or crenulate segments, and *P. choquetangense*, which has pinnatifid segments. All species have inconspicuously ciliate segment margins.

Whereas the segments are typically perpendicular to the rachis and straight or slightly falcate, several of the species (*P. absidatum*, *P. curvans*, *P. truncorum*, and *P. choquetangense*) have noticeably ascending segments (Fig. 3, C, D). In most species the segments have a symmetrical base in which both the lower and upper edges are dilated. However, in those species with ascending segments the upper edge meets the rachis abruptly at a nearly right angle. Also, several species, such as *P. atrum*, *P. paradiseae*, *P. pectinatiforme*, and *P. filicula*, have segments of the lower portion of the frond deflexed, and the lower edge of the segment correspondingly meets the rachis at a right angle or less (Fig. 3, B & Fig. 18). In *P. alfredii*, several plants from the northern part of its range have basal segments deflexed so that the lowermost segments are nearly or quite parallel to the stipe. There are several species, however, with all segments essentially at right angles to the rachis, but in which the lower edge of the segment meets the rachis at a right angle, or in which it may even be slightly incised to form a small sinus between rachis and basal margin (Fig. 3, A).

Figure 4 shows variations in the shape of the abaxial epidermal cells and the arrangement of the stomates. The cells over the lateral veins are characteristically narrower and more attenuated than those away from the veins. The stomates occur only on the abaxial surface. The guard cells are slightly elevated above the epidermal cells and are without modified subsidiary cells. Guard cell sizes, as they relate to the ploidal level, are discussed below.

The internal tissue of the segments is compact and quite uniform from one

species to another. They average approximately four layers of cells in the mesophyll (two to three in *P. truncorum* and five or six in *P. pectinatiforme*), two layers in a somewhat irregular palisade above and two (three, four) slightly less compact and more irregular layers in the spongy mesophyll (Fig. 1, D).

Figure 6 shows the representative range of venation patterns in the segments. Although the group typically has free-forked venation, three species (*P. filicula*, *P. siccum*, and *P. truncorum*) have simple veins. Entirely simple veins are not common in the *Polypodiaceae*, although the condition is frequent in the *Grammitidaceae*, a reason why *P. truncorum* has been considered as a ctenopteroid fern by Copeland (1956). However, on the basis of the spores, sporangia, trichomes, and the characters of the rachis, all three of these simple-veined species are properly members of the *Polypodium pectinatum-plumula* complex (de la Sota, 1963). Anastomosing venation, while not the rule in the present complex, occurs all through the *Polypodiaceae*. In the group under consideration here, anastomosing occurs in varying degrees from casual, irregular junctures in each segment, as in *P. pectinatum*, to very regular and complete patterns in *P. camptophyllum* var. *macedoi*. *Polypodium camptophyllum* var. *camptophyllum* has considerable variation, although it usually has at least a sporadic distribution of areoles. In some plants in southern South America the anastomosing in the latter variety becomes extensive and may even exceed that which is expected in var. *macedoi* (Fig. 6, Q, S). When anastomoses occur in this complex, they are always with a free included veinlet. This is opposed to the areolate condition in the *Grammitidaceae*, in which there are no included veinlets.

The costa, in all cases, is sclerified, sometimes only in the abaxial portion of the bundle sheath (e.g. *P. dispersum* and *P. pectinatiforme*), and sometimes throughout the bundle sheath, but then usually more so on the abaxial side, as in *P. truncorum* and *P. ptilodon* (Fig. 1, D). In several of the species with large fronds, the bases of the secondary veins are also sclerified. Except in *P. ferrugineum*, in which the costae are black and the rachis brown, the costae and rachis are the same color.

SORI

The sorus is terminal on the first acropetal veinlet in all species (Fig. 6). In those with anastomosing venation this veinlet becomes the free included veinlet. Whereas the sorus is typically medially or extra-medially placed on the segment, it may vary all the way from infra-medial (in *P. consimile*) to submarginal (in *P. sursumcurrens*, *P. alfredii*, and *P. paradiseae*).

Wilson (1959 a, b) has described in detail the sporangia of *P. plumula* and *P. ptilodon* var. *caespitosum* (as "*P. pectinatum*"). I have found these structures to be similar and with little deviation throughout the group. Although the annulus usually has 13 or 14 bow cells, *P. camptophyllum* var. *lachniferum* has only 12, and *P. sursumcurrens* and *P. curvans* have 16.

Wagner (1964) discusses and summarizes the known types of paraphyses in the ferns. Figure 4 illustrates the types found in this complex. Sori of all species produce receptacular paraphyses, and in all but two these are simple or occasionally

forked, multicellular, clavate hairs. In all but one species they are similar to the clavate laminar hairs, although they are often longer, and vary from 150-250 μ long. In *P. camptophyllum* var. *macedoi* the receptacular paraphyses are a curious mixture of the clavate and the acicular hair types (Fig. 4, M), being forked hairs with one clavate and one acicular branch. However, the same type of hair is also characteristic of the lamina. In *P. sursumcurrens* the paraphyses are unusual in differing considerably from the laminar trichomes (Fig. 4, P). They range up to 400 μ long. Their outline is contorted, and a multicellular, expanded portion is developed near the apex. In most species the receptacular paraphyses are few and hard to observe except by dissection and microscopic examination, but in *P. sursumcurrens* they are numerous and visible even with low magnification. Unlike the elaborate "sporangiasters" of *P. virginianum*, apparently derived from modified sporangia (Martens & Pirard, 1943), the paraphyses of *P. sursumcurrens* are evidently related to the simple, clavate, laminar hairs, as in the remainder of the complex.

Capsular paraphyses (Fig. 4) also occur in approximately half of the species of the complex. They are always short, simple, 1- to 3-celled hairs arising near the top of the capsule near the annulus. They vary in length from 45 μ in *P. pectinatum* to 100 μ in *P. hygrometricum*. They may be of quite regular number and occurrence—one per capsule in *P. pectinatum*; two in *P. hygrometricum* and *P. ferrugineum*; or of quite variable number, as in *P. dispersum* or *P. plumula*, in which they range from one to five per capsule. In several species they are present on young capsules but may be shed as the capsule matures.

SPORES

With two exceptions, spores in this complex are essentially alike. One exception, *Polypodium dispersum*, has only 32 mitotically produced, globose spores per sporangium. The other, *Polypodium camptophyllum* var. *camptophyllum*, has, for the most part, normal, reniform, tuberculate spores, but a few collections from Jamaica have quite irregular spores, which suggests that apogamous reproduction may be present in scattered populations of this species (see the taxonomic description of this variety).

The remaining taxa all have 64 spores per sporangium and are therefore presumed to have a normal sexual life cycle. The spores are uniformly reniform and monolete (Fig. 12, H), although they vary in shape from narrowly reniform and curved to globose-reniform. They are all without perispore and the surface is tuberculate, although the sculpturing varies from almost smooth to strongly tuberculate. The spore sizes, as they relate to the ploidal level, are discussed in the section on cytology and evolution.

GAMETOPHYTES

The gametophytes of *Polypodium dispersum* are so unusual that a separate section has been devoted to them in the section on sporogenesis. The gametophytes of the *Polypodiaceae* and *Grammitidaceae* have been treated by Stokey & Atkinson (1958), and the gametophytes of *P. plumula* and *P. ptilodon* var. *caespitosum*

(as "*P. pectinatum*") were reported by Stokey (1959). All my observations agree with those previously described.

The sex organs are typical of the *Polypodiaceae*, as described by Stokey. After fertilization the sporophyte plant is first seen as a tiny elliptic leaf (Fig. 2) and a root that appears either at the same time or slightly before the leaf. The leaves then develop as described above in the section on juvenile leaves.

ECOLOGY AND GEOGRAPHY

These ferns extend from Bermuda, peninsular Florida, northern Mexico and the Galápagos Islands south to northern Argentina and southern Brazil (Fig. 8, B). I consider them to occupy five distributional zones (Fig. 8, D): (1) Central America, (2) western South America, (3) southern Brazil, (4) northern and northwestern South America, and (5) the West Indies, considered a sub-zone of the last. As the distribution maps show (Fig. 8-11), several species occur in more than one zone, although a particularly large number of species are confined to the Central American and southern Brazilian zones. I have included the West Indies as a sub-zone of the northern South American zone because, out of the nine species present in the West Indies, six are known also in northern South America and do not occur in Central America. The remaining three species (*P. dispersum*, *P. plumula*, and *P. pectinatum*) are wide-ranging and cross several zones (Fig. 9, 10).

Although as a whole the genus *Polypodium* is primarily epiphytic, some species are terrestrial or epipetric. The same is true of the *P. pectinatum-plumula* complex. No species is strictly terrestrial, although *P. ptilodon* (including all its varieties) and *P. consimile* var. *consimile* are primarily terrestrial or occur on the bases of trees (Fig. 7, E). *Polypodium bermudianum*, *P. dispersum* (Fig. 7, A, G) and *P. ferrugineum* are primarily epipetric, although the two latter are recorded as occurring also epiphytically or terrestrially. *Polypodium choquetangense*, *P. curvans*, and *P. cupreolepis* are either epipetric or epiphytic. *Polypodium sursumcurrens*, *P. siccum*, *P. singeri*, and *P. truncorum* are evidently strictly epiphytic. *Polypodium singeri* is curious in that it apparently grows with its roots reaching the ground, so that it perhaps is only hemi-epiphytic. *Polypodium truncorum* has a particularly narrowly defined substrate, and is found only among the old stipe bases of tree ferns, especially *Alsophila* and *Hemitelia*. The remaining species are primarily epiphytic, but also occur occasionally as epipetric or terrestrial plants.

On the whole, this is primarily a group of tropical and sub-tropical montane plants. Elevation data indicates that they grow from 1500-3500 m in altitude, but a few species are found at low altitudes. *Polypodium dispersum*, *P. plumula*, and *P. ptilodon* var. *caespitosum* occur in peninsular Florida at nowhere over 100 m in elevation, although they are known elsewhere at much higher elevations. *Polypodium hygrometricum* and *P. recurvatum* are known only from sea level to 1800 m and *P. bermudianum* is confined to the low lying Bermuda Islands.

Certain of the epipetric species are recorded from exposed rocky areas or cliffs. No species grow in the lowland rain forests of the Amazon basin. Judging from the generally montane distribution, the response to drying (desiccation and curl-

ing of the frond without the death of the plant) and the articulate stipes, this group is not adapted to areas of constant high humidity, such as in the Amazon basin.

ECOLOGY OF ROOT PROLIFERATIONS

Several species in this complex reproduce partially by root proliferations; this appears to be related to their distribution and ecological requirements. Proliferations in *P. ferrugineum*, *P. filicula*, *P. siccum*, and *P. singeri* were found only on herbarium specimens, so it is difficult to note more than their mere presence. However, *P. singeri* normally grows as an epiphyte on small woody twigs. Several herbarium sheets show that the individual rhizomes are often short (ca 2 to 3 cm long) and grow in a series along the twigs (Fig. 7, D). The rhizomes and roots are exposed and the rhizomes arise as root proliferations.

Polypodium plumula and *P. pectinatum* grow either on the trunks or horizontal branches of trees, and are true epiphytes (Fig. 7, B). Root proliferations occur infrequently as small plantlets formed from the roots of larger plants. I have also observed small plantlets arising from the superficial roots of a greenhouse culture of the former species.

Although *P. dispersum* is capable of reproducing by spores (as discussed below in the treatment of sporogenesis), its primary mode of local dispersal is evidently by root proliferations. In Florida, for example, this species is usually seen as dense mats of juvenile plants completely covering limestone rocks (Fig. 7, G). Often none of these plants bear sporangia. I saw only three soriferous colonies of this species in the course of field trips in Florida, although I studied numerous populations.

The root proliferations in nature usually occur only a few centimeters apart when the plants are growing on rock surfaces. However, at "Blechnum Ravine" in Annatalaga Hammock, Florida, *P. dispersum* was growing in sand and the plants were widely spaced. In one case proliferations were spaced approximately 0.5 m apart on a very long root.

The rhizomes of these proliferations are always short and superficial on the substrate with no intermediate structure between parent root and rhizome, so that proliferations occur only on those roots that are close to the surface. As these seven species in which proliferations are known are all either epipetric or epiphytic, they normally grow where the substrate is thin and many of the roots are exposed or near the surface. These proliferations may be produced in response to reduced moisture or greater aeration around exposed roots. Increased light also might be a factor. However, the occurrence of proliferations in the dark at the bottom of the pot in greenhouse culture suggests that this is not so, unless a minimal exposure to light is sufficient.

SPOROGENESIS AND THE LIFE CYCLE OF POLYPODIUM DISPERSUM

I have carried out life cycle studies primarily on *P. dispersum* and *P. ptilodon* var. *caespitosum*. Experimental collections of *P. dispersum* have included a plant from Jamaica (Proctor 22896) and collections from Florida (Citrus Co, Wagner 62061, Evans 2008). Collections of *P. ptilodon* var. *caespitosum* have been from

Florida (Highlands Co, *Evans 1157*; Citrus Co, *Evans 2005*; Sumter Co, *Evans 2004*).

Sporogenesis studies were carried out using a modified acetocarmine squash technique. Segments with sporangia of a suitable age for meiotic figures were killed and fixed in Newcomer's Solution (Newcomer, 1953) and stored in a deep freeze until used. To prepare microscope slides, sporangia from a single sorus were placed in a drop of acetocarmine on a slide. No iron mordant was added, thereby avoiding overstaining of the cells. The sporangia were spread apart to avoid clumping, and a cover slip was added. The slide was heated slightly, but tapped only lightly with a dissecting needle in order not to spread the individual cells too far from the mother sporangium. Firm pressure was then applied with the thumb. The combination of few and wide-spaced sporangia, light tapping, and firm pressure with the thumb, resulted in preparations in which the cells were well squashed, but the individual cells of a particular sporangium were still in close proximity to each other. In this way numerous sporangia could be easily and quickly prepared and observed. The slides were made permanent by inverting them in 2:8 acetic acid: alcohol solution until the cover slips dropped off. After rinsing with the acetic acid-alcohol solution, the cover slips were replaced with a drop of diaphane.

In the *P. pectinatum-plumula* complex, the sexual life cycle (as determined by the number of spores per sporangium) is present throughout except in *P. dispersum*. In this common and widespread species, a pattern of apogamous reproduction thus far unique among pteridophytes has been found.

SEXUAL LIFE CYCLE

The sexual life cycle of the higher ferns is well known. In comparing this with apogamous reproduction, it is only necessary to summarize the process of sporogenesis in a sexual species, as exemplified by *P. ptilodon* var. *caespitosum* (Fig. 12). In the developing sporangium, the archesporial cell divides mitotically four times to form 16 2 $\times$ spore mother cells (Fig. 12, B). The spore mother cells are readily recognized by their size and form, and also by the large, darkly staining nuclei. They undergo one meiotic division (Fig. 12, C, D) to form a tetrad of young spores (Fig. 12, E-G), resulting in 64 monolete spores per sporangium (Fig. 12, H). Upon spore germination and maturation of the bisexual gametophyte, fertilization may occur; the sporophyte plant develops from the fertilized egg, thus completing the cycle.

OBLIGATE APOGAMOUS (MEIOTIC APOGAMOUS) LIFE CYCLE

Although not so widely known as the sexual life cycle, this process is well documented, as in several papers by Döpp (c.f. 1939) and later by Manton (1950) and others.

Using herbarium specimens, apogamy can usually be detected by making preparations of mature but unopened sporangia. Some of the sporangia, if the plant is apogamous, will have 64 aborted spores, whereas others will show 32 normal-appearing spores.

Apogamous reproduction is normally a process in which sporogenesis is modified and sexual fusion is by-passed. It always involves plants with an unbalanced genotype that could not, in the usual sexual cycle, form viable spores. The process is known in many species of ferns and is considered to be quite widespread. Wagner (1963) estimates that approximately 7% of the 72 pteridophytes of Giles Co, Virginia, U. S. A., reproduce apogamously. Mehra (1961) found 30 apogamous ferns among 350 cytologically known ferns from the Himalayan region, or about 8.6%. The highest frequency of obligate apogamy is among triploids, although apogamy is known at other ploidal levels, including the diploid (Mehra *loc. cit.*).

In order to compare the apogamous situation in *P. dispersum* with the more usual apogamous sporogenesis, the following brief outline of the latter will provide a comparison. In obligate apogamy the $2\times$ archesporial cell in certain developing sporangia divides mitotically three times forming 8 cells. There is then a further chromosomal division without cytokinesis, and a reorganization of the genetic material into single nuclei ("restitution nuclei"). This results in eight $4\times$ spore mother cells from the initial $2\times$ archesporial cell. Meiosis in these doubled cells is then normal, but produces only 32 viable $2\times$ spores per sporangium.

It should be added that these meiotic apogamous ferns usually also undergo spore formation in another way. In some sporangia, the spores develop without the formation of restitution nuclei. This is essentially the process of sporogenesis in sexual species. However, because of the hybrid-like behavior of the chromosomes in apogamous ferns, in which the genomes do not pair normally except in the restitution nuclei, this process results in irregular and aborted spores.

According to Manton (1950) these two processes can occur in different sporangia on the same apogamous plant, in the same or different sori, and in quite varying proportions, from only a few 32-spored sporangia per sorus to many sporangia of this type per sorus.

The spores produced from 32-spored sporangia develop into gametophytes which usually form sex organs. The archegonia are aborted, or may be absent; but the antheridia and sperms may be functional. The new sporophyte develops not from the sexual apparatus but directly from thallus tissue.

AMEIOTIC ALTERNATION OF GENERATIONS IN POLYPODIUM DISPERUM

Obligate meiotic apogamy has been considered the only successful or functional apogamous life cycle in ferns, and Manton (1950) termed the process as "monotonously uniform." However, in the *P. pectinatum-plumula* complex, *P. dispersum* displays a unique alternative in apogamous reproduction in ferns (Evans, 1964).

A study of sporogenesis in *P. dispersum* (Fig. 13) shows four complete mitotic divisions of the archesporial cells to form 16 spore mother cells in *all* sporangia, without restitution nuclei. The 16 spore mother cells are readily visible, for they separate, enlarge, and stain more darkly than other cells in the sporangium (Fig. 13, C). All sporangia observed contained only 32 spores. This involved the observation of several hundred sporangia both in sporogenesis studies and on herbarium specimens. In metaphase figures *Polypodium dispersum* has 111 unpaired

chromosomes (Fig. 13, E). Squashes of metaphase figures in the eight-celled stage of the archesporium and in the 16 spore mother cells show that the chromosome configuration is essentially identical, both stages showing 111 unpaired chromosomes (Fig. 13, A, D). The mode of cytokinesis of the 16 spore mother cells (Fig. 13, F, H) indicates that each mother cell produces only 2 spores.

The spores are thus formed by one additional mitotic division of the spore mother cells, and meiosis, characteristic of all other known apogamous ferns, is absent (hence my distinction of the two types of apogamy as "meiotic" and "ameiotic"). This is an example of diplospory. Mehra (1961) reports that "diplospory which is so widespread in apomictic angiosperms has so far not been observed as a functional mechanism in apomictic ferns, although there are stray records of its occurrence." Reports of *Trichomanes proliferum* forma β (Bell, 1960; Mehra & Singh, 1957) and in *Ophioglossum* and *Isoetes* (Verma, 1956, 1960) suggest that this process may also occur in pteridophytes other than *P. dispersum*. However, none of the latter reports contain information pertaining to the gametophyte generation or whether or not these plants are capable of completing their life cycle. Braithwaite (1964) indicates a similar situation in *Asplenium aethiopicum* to that observed here. He describes the formation of 32 spores from 16 spore mother cells as being due to a partial meiotic division and a restitution nucleus. These would appear to be very similar processes in these two different genera.

The irregularities in this process are few. There are occasional sporangia which contain a lower number than 32 spores and some spore fragments. Occasionally, mature spores are contracted medially or submedially as though the cell had begun to divide again. I do not yet know whether these "pinched" spores are viable. In the examination of several hundred divisions only one cell was found that may have doubled its chromosomes. As I obtained over 60% germination of spores, I am quite sure that these few irregularities contribute little or nothing to this germination percentage, and that the viable spores are formed as outlined above.

The morphology of the *Polypodium dispersum* spore is a further departure from the norm. All other species in this complex have the usual reniform, monolete, polypodioid spores, which are formed in tetrads.

The *P. dispersum* spores, in contrast, are distinctly globose, and the scar is exceedingly variable, being either incomplete or suggesting a monolete or trilete pattern (Fig. 14). Occasionally the scar is absent. Spores of apogamous ferns normally resemble the spores of closely related species. In the surface tuberculation, spores of *P. dispersum* are like those of related species, but in the spore and scar shape they are readily distinguishable microscopically.

In agar plates fortified with Knop's Solution, and grown under constant light at 20°C, spores germinated in about 10 days, and development was rapid; young apogamous sporophytes forming in about two and a half months.

The first rhizoid appears with, or even before, the first prothallial cell (Fig. 2, A), and subsequent rhizoids develop with each additional cell, often more than

one rhizoid per cell. After one to three filamentous cells develop, an elliptical plate is formed, and rhizoid initiation is reduced.

The cell plate of *P. dispersum* is not cordate, as are most polypodioid gametophytes. At the time of sporophyte proliferation the prothallus is either small and elliptical (Fig. 15, G), or it may be strap-shaped and several times branched (Fig. 2, D). The latter is typical of artificial cultures. In nature, both small elliptical thalli, not much larger than the bases of the sporophytic proliferations, as well as longer, branched thalli are found. Rhizoids are either marginal or near the margin. If the thallus is branched, rhizoids are usually more dense at the confluence of the branches. They are never wholly basal and ventral, as is normal in other sexual species of *Polypodium*. The shape of the thallus and the position of the rhizoids suggest that *P. dispersum* has gametophytes like those of the *Grammitidaceae*. However, the early development of both the rhizoids and the cell plate are characteristically polypodioid. Also, the rhizoids of *P. dispersum* are a light brown, not dark brown and stiff, as is typical of the *Grammitidaceae* (Stokey & Atkinson, 1958).

Two features of *Polypodium dispersum* gametophytes are unique: the absence of gametangia and the ability to produce stomata on a thallus one cell thick. Previously known apogamous ferns produce sex organs even though they are not functional in self-reproduction. No sex organs were observed in either wild or cultured collections of *P. dispersum* gametophytes.

Stomates were observed on several of the gametophytes that had already proliferated sporophytes. As the thallus is everywhere only one cell thick, the stomatal apparatus merely consists of two typical guard cells over an opening between thallus cells (Fig. 2, B & Fig. 15, D, E). Its function, if any, is unknown.

Stomates have previously been observed on apogamous gametophytes (Steil, 1919), but always at the base of the sporophyte and associated with cells already modified in morphology toward sporophytic epidermal cells (elongate and with undulate lateral walls). However, in *P. dispersum*, these stomates occur on lobes without sporophytes (although always on gametophytes containing proliferations) and in tissue with cells still strictly of gametophytic structure.

The sporophytic proliferation in *Polypodium dispersum* is first noticeable as a small swelling on the dorsal surface, usually near the margin of the thallus (Fig. 2, 15). In the very small, elliptic gametophytes it arises from the center and quickly occupies all but a small fringe of gametophyte tissue around the base of the small sporophyte plant. This swelling very early produces both the simple and ctenoid, clavate hairs of the juvenile sporophyte (Fig. 15, D, F, G). The swelling may be only a few cells high or it may become 1 or 2 mm long before differentiation takes place at the apex. A fine strand of two or three partially over-lapping, spirally thickened tracheids appears in a central core of narrow cells in the swelling. One or two tiny strap-shaped leaves with a delicate midrib, marginal acicular hairs and simple and ctenoid laminar hairs arise, followed by a series of leaves like those of sexually produced and root proliferated sporophytes. The first leaf (and sometimes the second) appears before the roots. This is in contrast to the sexually

produced sporophyte, in which the first root appears with or usually before the first leaf.

As in any obligate apogamous fern, the ameiotic apogamous cycle of *P. dispersum* allows dispersion and colonization without the necessity of fertilization. It is unique, however, in that the cycle has entirely the character of sexual reproduction with neither meiosis nor syngamy and the usual associated opportunities for genetic assortment and recombination. At the same time that meiosis and syngamy of the sexual cycle are missing, syndiploidy and meiosis of the meiotic apogamous cycle are also missing. The only way to inject changes into the genome of *P. dispersum* would be by random mutation and selection for or against this mutation. But any mutations selected would then be carried by all spores of the plant. Consequently, one might expect that this species would have a limited ecological and geographical potential. Yet this species is frequently collected and is widespread in the New World tropics (Fig. 9). Morphological variation from one individual to another is about as great as in most of its relatives. There is even one distinctive collection of numerous specimens (*Wright 1051*) with incised segments from Cuba, where the typical form is common. In spite of its seemingly limited genetic potential, its somatic life cycle has evidently been quite successful in adapting this species to its environment.

CYTOLOGY AND EVOLUTION

One of the major efforts in recent systematic studies of the *Filicineae* has been to subdivide the classical all-encompassing and undoubtedly polyphyletic family *Polypodiaceae*. Serious attempts at a more natural arrangement have led to such revisions as those of Bower (1923), Christensen (1938), Ching (1940), Dickason (1946), Copeland (1947), Holttum (1947, 1949), Alston (1956) and Pichi-Sermolli (1959). Within the *Polypodiaceae sensu stricto* there has been, at the same time, a subdivision of the classical genus *Polypodium* into presumably more natural genera. Today there is a general agreement as to the extent of the genus *Polypodium*, although Copeland (1947) segregated out *Goniophlebium* Presl, a step I do not think warranted on present evidence.

The *Polypodium pectinatum-plumula* group is more similar in certain gross appearances to *Ctenopteris* in the *Grammitidaceae* than to the rest of the genus *Polypodium* as a whole—so close, indeed, that Copeland (1956) placed *P. truncorum* in *Ctenopteris* and suggested that *P. pectinatum* and *P. plumula* might also belong there. Copeland's paper inspired critical studies of the sporangia (Wilson, 1959 a, b) and gametophytes (Stokey, 1959) of the latter two species. Table 1 lists character differences between this complex and the *Grammitidaceae*.

I believe that these families, based primarily on the differences in spores, sporangia, paleae, and gametophytes, should be maintained, although there still remain vexing problems as to their origin. There are, basically, two lines of thought—one that the *Grammitidaceae* arose from the *Polypodiaceae* (Pichi-Sermolli, 1959; Christensen, 1938), and the other that the *Grammitidaceae* arose independently from gleichenioid stock (Holttum, 1947, 1949; Stokey, 1951; Copeland, 1947). There are also dual propositions as to the origin of the *Polypodiaceae*,

Table 1. Comparison of the *Polypodium pectinatum-plumula* complex with the *Grammitidaceae*.¹

<i>P. pectinatum-plumula</i> complex	<i>Grammitidaceae</i>
SPOROPHYTE:	
<i>Rhizome</i>	
Creeping, short-creeping, or erect	Short, ascending
Paleae non-clathrate (rarely sub-clathrate), entire or partially and inconspicuously papillate or fimbriate	Paleae clathrate or not, often conspicuously setose
<i>Frond</i>	
Stipe usually articulate	Stipe rarely articulate
Rachis always paleate (often inconspicuously)	Rachis never paleate
Short-spaced or approximate to fasciculate	Mostly fasciculate
Lamina usually with flexuous or stiff multicellular acicular hairs	Lamina usually with long, stiff, unicellular or multicellular setose hairs
Venation forked (rarely simple), free, or if anastomosing, then with free included veinlet	Venation simple (sometimes forked), free, or rarely anastomosing without included veinlet
Sporangial stalk with 2-3 columns of cells	Sporangial stalk with 1 column of cells
Spores bilateral, monolete, golden (without chlorophyll)	Spores tetrahedral, trilete, green (with chlorophyll)
GAMETOPHYTE:	
Cordate, with ventral rhizoids (rarely strap-shaped with marginal rhizoids)	Strap-shaped, with marginal rhizoids
Rhizoids appearing with first prothallial cell, or later	Rhizoids appearing after 10-15 prothallial cells have appeared
Plate early forming (after 1-2 months)	Plate late forming (after 2 months- 1 year)
Simple papillate hairs common	Simple papillate hairs uncommon
Branched hairs uncommon	Branched hairs common

¹Compiled from personal observations and those of Copeland (1947, 1956), Stokey (1951, 1959), Stokey & Atkinson (1958), Wilson (1959 a, b), and de la Sota (1960).

one that they arose from dipteroid stock (Holttum, 1947, 1949; Pichi-Sermolli, 1959), the other that the *Polypodiaceae* also arose from gleichenioid stock (Copeland, 1947; Stokey, 1951). The origin of the *Grammitidaceae* from gleichenioid ancestors appears to have much support in actual resemblances, i.e. the trilete spores, free forked or simple venation, and the rather stiff pectinate blades. It has been argued that the *Polypodiaceae* arose from dipteroid stock through forms like

Dipteris, *Matonia*, and *Cheiropleuria*, which have complicated stelar anatomy and anastomosing venation. However, one can also read the opposite sequence from gleichenioid stock to the free-veined polypodia, perhaps much like the present members of the *P. pectinatum-plumula* complex. One of several difficulties in tracing evolutionary patterns in *Polypodium* is that of the free vs. anastomosing venation. Christensen (1928) builds a case for the origin of free venation in the

Table 2. Chromosome observations.

Taxa, with collection & location	Number
<i>P. alfredii</i> Rosenst.—Mexico, Oaxaca, Zacatepec, Mickel 1613; Costa Rica, Guanacaste Prov, Evans 2890.	$n=37$
<i>P. bolivianum</i> Rosenst.—Costa Rica, Alajuela Prov, Evans 2921, Puntarenas Prov, Evans 3155, 3057-1.	$n=37$
<i>P. camptophyllum</i> Fée var. <i>camptophyllum</i> —Jamaica, Portland Parish, Evans 2404, 2405, 2406, 2407, 2408, 2409, 2410, 2413, St. Andrew Parish, Evans 2378.	$n=74$
<i>P. camptophyllum</i> Fée var. <i>lachniferum</i> (Heiron.) Evans—Jamaica, St. Andrew Parish, Evans 2440, St. Thomas Parish, Evans 2637-13.	$n=74$
<i>P. dispersum</i> Evans—Florida, Citrus Co, Evans 2007, 2008, Wagner 62061, Hillsborough Co, Evans 1189, 2019; Jamaica, Portland Parish, Evans 2400, 2402, 2403, Proctor 22896.	" $2n$ "=111
<i>P. ferrugineum</i> Mart. & Gal.—Mexico, Nayarit, Ceboruco volcano, Mickel 1374.	$n=37$
<i>P. hygrometricum</i> Splitg.—Costa Rica, Puntarenas Prov, Evans 2733.	$n=37$
<i>P. paradiseae</i> Langsd. & Fisch.—Brazil, Rio Grande do Sul, São Leopoldo, Sehnén s.n.	$n=37$
<i>P. pectinatum</i> L. s.s.—Jamaica, Portland Parish, Evans 2534-1, Trelawny Parish, Evans 2588; Costa Rica, Alajuela Prov, Evans 2984-1.	$n=37$
<i>P. plumula</i> Humb. & Bonpl. ex Willd.—Florida, Hernando Co, Wood, s.n., Hillsborough Co, Evans 1186, Sumter Co, Evans 1190, 1192, 1193; Jamaica, Portland Parish, Evans 2398.	$n=74$
<i>P. ptilodon</i> Kunze var. <i>caespitosum</i> (Jenm.) Evans—Florida, Dade Co, Delchamps 6/14/60, Hernando Co, Evans 2015, Highlands Co, Evans 1158, Hillsborough Co, Evans 2018, Sumter Co, Evans 2002, 2003; Jamaica, Portland Parish, Evans 2411, 2412, 2414; Mexico, San Luis Potosi, Xilitla, Mickel 602.	$n=74$
<i>P. ptilodon</i> Kunze var. <i>ptilodon</i> —Peru, Prov Bagua, Dept Amazonas, Hutchison 1470.	$n=37$
<i>P. recurvatum</i> Kaulf.—Brazil, Rio Grande do Sul, São Leopoldo, Sehnén s.n.	$n=37$
<i>P. siccum</i> Lindm.—Brazil, Rio Grande do Sul, São Leopoldo, Sehnén s.n.	$n=37$

P. vulgare group from the goniophleboid venation. In the group under present study there are several species with partial to almost complete reticulation, species which are also pubescent, as are most of the truly goniophleboid species. These reticulate venation patterns could be considered as either generalized or specialized character states, but are here treated as examples of a condition derived from free venation. The interpretation of this character is involved with the interpretation of the origin of the family, either from free-veined gleichenioid stock or anastomosing dipteroid stock. The answer is not immediately self-evident.

CYTOLOGY

Fourteen taxa were available for chromosome counts (Table 2). These are too few to be of application in interpreting the whole picture of speciation in the complex; however, all counts are useful. It was initially assumed that *Polypodium dispersum* was a hybrid between *P. plumula* and *P. ptilodon* var. *caespitosum*, but chromosome counts indicate that this is not likely. In the case of *P. ptilodon* var. *ptilodon* and var. *caespitosum*, a difference in their chromosome counts helps in interpreting them as at least separate varieties. *Polypodium ferrugineum* is quite similar to *P. cupreolepis*, except that the former has larger spores. It might have been considered a tetraploid derivative of *P. cupreolepis*, were it not known to be a diploid.

Table 3 indicates mean spore and guard cell lengths (based on 10 measurements per specimen and 3-10 specimens of each species or variety). Those cytologically known taxa have their ploidal level also indicated. On the assumption that spore and guard cell length are usually affected by polyploidy, this can give some indication of possible ploidal levels in certain of the species. Unfortunately, there are not enough cytologically known taxa to give real indications of such levels, but certain suggestions can be made. The taxa are here arranged in descending order of length of spores.

In this table there is some indication that those taxa with guard cell lengths of ca 45μ or greater, correlated with a spore length of 50μ or greater, may be polyploids. Conversely, those taxa with guard cells less than 40μ long, correlated with spore lengths of less than 47μ could be expected to be diploids. On this basis it is predicted that those taxa marked with an (*) are probable polyploids, and those marked with an (o) are expected diploids.

DIVERGENCE INDEX AND COMMON GROUND PLAN

The relationships of the *P. pectinatum-plumula* complex are diagrammed in Fig. 16. This is a method for expressing evolutionary relationships developed by Wagner (1961, 1962), at the University of Michigan and used by such previous authors as Hardin (1957), Mickel (1962), and Scora (1964).

A list of as many characters as possible that show contrasting character states within the complex is first compiled. The generalized and the specialized state of each character is indicated. This is ascertained by noting the frequency and distribution of a certain character state. The assumption is that the more common the character state the more likely it is to be the generalized state. It is necessary

Table 3. Comparison of spore and guard cell size and chromosome number.

Taxon	Spore length in μ	Chromosome number	Guard cell length in μ
* <i>P. absidatum</i>	59		66
* <i>P. ptilodon</i> var. <i>robustum</i>	56		52
var. <i>caespitosum</i>	56	$n=74$	50
* <i>P. camptophyllum</i>			
var. <i>lachniferum</i>	54	$n=74$	57
var. <i>camptophyllum</i>	54	$n=74$	52
<i>P. pectinatiforme</i>	52		39
* <i>P. venturii</i>	50		65
<i>P. filicula</i>	50		41
° <i>P. ferrugineum</i>	50	$n=37$	40
° <i>P. alfredii</i>	50	$n=37$	37
* <i>P. plumula</i>	50	$n=74$	34
<i>P. sursumcurrens</i>	49		38
<i>P. ptilodon</i> var. <i>pilosum</i>	47		44
° <i>P. hygrometricum</i>	47	$n=37$	39
° <i>P. pectinatum</i>	45	$n=37$	47
<i>P. truncorum</i>	45		41
° <i>P. siccum</i>	45	$n=37$	37
<i>P. eurybasis</i> var. <i>glabrescens</i>	44		44
var. <i>villosum</i>	44		43
<i>P. curvans</i>	44		43
<i>P. camptophyllum</i> var. <i>macedoi</i>	44		43
<i>P. bermudianum</i>	43		43
° <i>P. bolivianum</i>	43	$n=37$	43
° <i>P. recurvatum</i>	43	$n=37$	39
<i>P. dispersum</i>	43	" $2n$ "=111	38
<i>P. camptophyllum</i>			
var. <i>abbreviatum</i>	43		43
° <i>P. paradiseae</i>	42	$n=37$	43
<i>P. choquetangense</i>	42		50
° <i>P. ptilodon</i> var. <i>ptilodon</i>	41	$n=37$	40
<i>P. eurybasis</i> var. <i>eurybasis</i>	40		50
<i>P. consimile</i> var. <i>consimile</i>	40		43
var. <i>pastazense</i>	40		40
° <i>P. cupreolepis</i>	36		31
° <i>P. atrum</i>	34		35
<i>P. singeri</i>	32		45

to test this assumption by taking into account related taxa or groups of taxa outside the one in question. In the analysis of a genus one must thus examine other closely related genera. In the present case, members of the genus *Polypodium* outside the complex were considered. In this way, it is possible to evaluate with strong probability a character state which appears frequently in a given group, but which may actually be a derived character state when taking the overall group into consideration.²

²The polished aspect of the rachis of the *P. pectinatum-plumula* complex is present throughout the group and might therefore be considered as generalized. However, this is

An initial list of characters, each showing paired character states, was selected. However, certain of these characters did not appear to have direct evolutionary significance; they had no obvious correlations. To simplify the diagram and reduce the information to the most definite characters and trends, these fluctuating characters were eliminated from the ground plan.

Each of the remaining 23 characters was then evaluated as to whether it is a generalized or specialized character state, the generalized state being given the value (0), and the derived state (1). This is based on the principle that, as we do not really know any actual quantitative value for a specific character, it is best to give them all equal values. In two characters—pinnatifid vs. crenate or entire segments, and comose hairs obscuring the rhizome paleae vs. comose hairs few or absent—however, I have given a value of 1.5 to these isolated and exaggerated expressions of an already specialized character state. Also, in evaluating the character of basal segments perpendicular to the rachis (0) or deflexed (1), I have added an intermediate level (0.5) for those cases which have a sporadic expression of the specialized state. Such situations could be avoided by establishing additional characters for these conditions, e.g. segments pinnatifid (1) versus segments crenate (0). But considering that the “ultra” specialized character state 1.5 in each case occurred in species obviously related to other species exhibiting the specialized character state 1, this seemed to be the clearest path to take. The same is true of the intermediate 0.5 state.

The total values of the character states for each entity are totaled, giving each a quantitative index showing its approximate divergence from the hypothetical ancestor, which had all the characters in the generalized state. This value then indicates at which level, i.e. on which semicircle on the divergence figure, the species will be placed. The position depends on the correlation of as many derived character states as possible from one species to another. Where it is necessary to cause a line to fork and there is no extant plant which “fits” this position, a “hypothetical ancestor,” or “prototype” to those following it on the lines (indicated by open dots in Fig. 16) is inserted. This brings out an interesting point regarding the use of these “hypothetical ancestors” within a very closely related group of plants. Mickel (1962), in constructing a ground plan for the species of the genus *Anemia*, subgenus *Coptophyllum*, had to use 19 “hypothetical ancestors” in evaluating 41 taxa. Scora (1964) had to use 13 “hypothetical ancestors” in placing 22 taxa in the genus *Monarda*. Yet in the present study, in placing 35 species, only 8 were necessary. This may be due to the wider spread of morphological diversity that usually occurs in the species of a whole genus or subgenus, as compared to a single species complex within a genus. In the present study the species are

not so elsewhere in *Polypodium* and is therefore considered a derived character state. In the same way, the *black* polished rachis is considered a derived character state, as it occurs with less frequency than the red-brown polished rachis. In the case of the polished versus non-polished rachis, this character is not used at all in the ground plan analysis because this character state is present throughout the group and therefore has no evolutionary significance within the complex, though it might well have significance in an evaluation of the whole genus or family.

recognized to be closely related, and therefore the divergence pattern reflects this closeness in that many species appear to be directly related in a linear or diverging series.

The following are the evaluations of the characters used in formulating the common ground plan:

A. *Rhizome*: Throughout most of the genus, as well as the family, the rhizome is long-creeping. In this complex several of the species of smaller stature, particularly those allied with *P. plumula*, have a more specialized, short-creeping, sub-erect or erect rhizome.

B.-C. *Rhizome Paleae*: The generalized shape of the paleae is narrow- or linear-triangular. However, in several of the species, e.g. *P. cupreolepis*, *P. alfredii*, *P. ferrugineum*, *P. sursumcurrens*, and *P. filicula*, the paleae are ovate or cordate (B). One of the specialized features of practically the whole complex is the comose rhizome paleae (C) (Fig. 1). Inconspicuously comose paleae also occur in several species not closely allied to this complex as judged by other characters, which have been excluded from the present treatment. There are a few of the included taxa allied with *P. plumula* which characteristically lack this comose condition. Since palear comosity is probably specialized, those species which have not developed it are considered generalized in this respect.

D. *Rachis Color*: The rachis is lustrous or polished, and though this is undoubtedly a specialized condition, it is a null character as far as divergence within the complex is concerned. However, there are essentially two color phases: red-brown in the *P. pectinatum* allies and either red-brown or black in the *P. plumula* allies. As stated above, the black condition is considered specialized.

E.-F. *Rachis Firmness*: Though most of the group have a stiff and erect rachis, as do most species of *Polypodium* in general, several members have specialized springy elastic rachises, readily recognizable on herbarium sheets (E). There are also two species, *P. curvans* and *P. choquetangense*, that show an additional specialization in the twisting or curling of the rachis under normal growth conditions (F). (This is not to be confused with the curling of the rachis and costa causing the frond to curl up under dry conditions.)

G. *Rachis Pubescense*: Although the whole group is characterized by a variety of types of rachis trichomes, and the rachises vary from nearly glabrous to pilose, *P. eurybasis* var. *villosum* has a striking densely-villose rachis distinguishing it from all other species.

H. *Ctenoid Hairs of the Rachis*: Although inconspicuous ctenoid hairs can probably be found on any species of *Polypodium*, at least on juvenile fronds, the species of the *P. pectinatum* group are noteworthy because of the numerous, large, conspicuous ctenoid hairs developed also on the mature rachis (Fig. 1, F). This is considered a specialized condition.

I. *Rachis Paleae* (Fig. 5): Though the rachis paleae vary considerably throughout *Polypodium*, in this complex and in those polypods most similar to those of this complex, the inconspicuous, long, thin, filiform type of palea is most frequent and therefore considered primitive. However, a number of species allied with *P. plumula* exhibit numerous hastate-triangular or cordate, conspicuous paleae on the

rachis, which are probably specialized. They are either concolorous or have a dark margin and paler base (Fig. 1, H) and are thus different from the clathrate paleae with pale margins in the *P. squamatum* and *P. vulgare* groups.

J. *Fronde Size*: Though there is considerable size variation in *Polypodium* (Fig. 3), there are a few species which are significantly reduced in size. These are represented here by *P. ferrugineum*, *P. filicula*, and *P. camptophyllum* var. *abbreviatum*, which have fronds generally less than 25 cm long.

K. *Length of the Stipe*: Whereas the majority of the species of *Polypodium* have a well-defined stipe that is readily distinguishable from the rachis, several species have the specialized condition of sessile or nearly sessile blades, as represented in the *P. pectinatum-plumula* group by *P. consimile*, *P. filicula*, and *P. ptilodon* var. *pilosum*.

L. *Blade Base*: The most general blade outline in *Polypodium* is elliptic-ovate, or linear with a cuneate or subtruncate base. However, several species, here represented by *P. bolivianum* and *P. recurvatum*, have a specialized, very abruptly truncate blade base (Fig. 3, G).

M. *Basal Segments*: Most polypodioid ferns have segments that are all essentially perpendicular to the rachis, and this is considered a generalized character. Certain species, however, show a distinctly different orientation at the base of the blade, with the basal segments becoming increasingly deflexed (Fig. 3). This usually creates an asymmetry at the segment base in which the upper edge meets the rachis at a broadly confluent angle, whereas the lower edge meets the rachis at a much sharper angle (see character 0). Species with basal segments irregularly deflexed are given an intermediate value of 0.5.

N. *Segment Orientation*: Pinnatifid polypodioid ferns commonly have either straight or slightly falcate segments which are essentially perpendicular to the rachis or slightly ascending (usually not more than 20° above the horizontal). The group of *P. absidatum*, *P. curvans*, and *P. choquetangense* have distinctly ascending segments exceeding ca 30° above the horizontal (Fig. 3, C).

O. *Segment Base Symmetry*: The segments of pinnatifid polypodioid ferns usually have an essentially symmetrical base, expanded and confluent on the rachis. In several species of this complex the lower edge of the segment meets the rachis at a right angle or may even be partially incised on the lower side, creating a semi-pinnate condition. This character has only been considered as specialized, however, when the segments are at right angles to the rachis (Fig. 3, A). When the segments are either ascending or deflexed this is automatically reflected in an asymmetry at the base.

P. *Segment Margin*: Whereas the majority of these species have the generalized condition of segments with entire margins, the species allied to *P. eurybasis* and the *P. curvans*—*P. choquetangense* line have crenate margins, as do *P. paradiseae* and *P. sursumcurrens* (Fig. 3, Fig. 6). In *P. choquetangense* (Fig. 6, T) the segments are deeply pinnatifid, and I have assigned this character state the "ultra" value of 1.5.

Q.-R. *Laminar Pubescence*: This refers only to the relatively conspicuous acicular, non-appressed hairs, since all members of this group have inconspicuous

clavate hairs. The presence of a conspicuous pubescence is considered derived from the essentially glabrous condition (Q), and the presence of definite patterns of distribution of these hairs, as in the *P. ptilodon* group (Fig. 1, E), is considered an additional derived character state (R).

S. *Lateral Veinlets*: The great majority of polypodioid ferns have either anastomosing or free forked venation patterns. However, the specialized state of simple venation is present in this group in *P. truncorum*, *P. siccum*, and *P. filicula* (Fig. 6).

T. *Sorus Position*: In the free veined species of *Polypodium* the sorus is always terminal on the first acropetal veinlet and is usually medial between the costa and the laminar margin (Fig. 6). However, in several instances, the fertile veinlet typically extends almost to the margin, thus reflecting the condition of comparable veinlets in a sterile segment. In these instances the sori are then marginal or submarginal, and this is considered a derived character state.

U. *Receptacular Paraphyses*: In almost all taxa the receptacular paraphyses are composed of uniform cells and are similar to the clavate hairs of the lamina, though they are occasionally branched. They are universally present in this complex, and in most of the species examined in the rest of the genus and the family *Polypodiaceae*, and so it is believed that this simple paraphysis type is generalized. However, *P. sursumcurrens* exhibits an unusual paraphysis with an irregular subterminal multicellular clavate head (Fig. 4, P). As the head is composed of undifferentiated, though contorted, cells, it is considered to be derived not from reduced sporangia ("sporangiasters" as in *P. virginianum*), but from coalesced cells of a strongly twisted simple type of paraphysis. *Polypodium camptophyllum* var. *macedoi* exhibits another distinctive paraphysis type; this is regularly forked, but one fork is tipped by a clavate cell, the other by a sharply setose cell (Fig. 4, M). The small appressed hairs of the lamina of this species are similar to the paraphyses.

V. *Spore Length*: While great length may be a simple morphological specialization by itself or reflect polyploidy, in either case it represents a divergence from the ground plan and is thus considered specialized.

W. *Number of Spores Per Sporangium*: In the higher ferns, 64 spores per sporangium is a regular occurrence and has become a standard for indicating the normal sexual life cycle. Similarly, 32 spores per sporangium indicates an apogamous asexual reproduction, as is the case in *P. dispersum*. Apogamy is considered a specialized type of life cycle.

TAXONOMIC REVISION OF THE POLYPODIUM PECTINATUM-PLUMULA COMPLEX³

In treating this group of closely related species of *Polypodium*, there are no clear-cut limits in inclusion and exclusion. The species here included are circumscribed by the characters of blades with pectinate segments, essentially free veins, approximate to fasciculate fronds, rigid or elastic, lustrous, red-brown or black stipe and rachis, triangular and comose or cordate and non-comose, non-clathrate

³Until a broad and thorough examination of all the species-complexes in *Polypodium* are made, it seems wisest to withhold a formal subgeneric or sectional designation for this complex.

rhizome scales, 2-3 rowed sporangial stalks, and reniform spores. The species of closest superficial resemblance in *Grammitidaceae* are excluded on the basis of the sporangial stalk, spores, and other characters (see Table 1 above). Certain species of *Polypodium* have been excluded that might, in a wider treatment of the whole genus, be included here in the future. *Polypodium hartwegianum*, *P. chnoophorum*, *P. moritzianum*, and others have inconspicuously comose rhizome scales but have been excluded on the basis of the lack of the lustrous rachis, the different texture of the lamina, or the more crisped silvery laminar trichomes. I have, on the contrary, included *P. hygrometricum* and *P. recurvatum*, which perhaps are more properly placed with these excluded species. However, the latter two have been particularly confused with the included species both as to taxonomy and nomenclature. Future work should be directed at delimiting the different groups (possibly as subgenera) within *Polypodium sensu stricto* so that all the species can eventually be grouped and treated systematically.

The measurements of rhizomes, fronds, blades, and segments include a mean size bracketed by an expected maximum and minimum limit. These were compiled by measuring ten random specimens of each recognized entity. "Ctenoid hairs" refer to small, appressed, multiple-branched hairs with all the branches arising from one side of the main axis (Fig. 1, F & Fig. 4, I). "Comose" rhizome paleae refer to those with tufts of unicellular hairs arising from the dorsal surface (Fig. 1). The costa is "decurrent on the rachis" when it joins the rachis in a downward arc to form a short wing along the rachis and a visible curvature of the costa. When the costa meets the rachis at a right angle, there is also a slight expansion on the rachis but no visible curvature of the costa. In defining plane shapes (e.g. fronds, segments, scales), I have attempted to follow the Systematics Association, Descriptive Terminology, Chart 1 (Taxon 11: 145-156, 1962), with the addition of the term "cordate," as it so usefully applies to the overall shape of many paleae (Fig. 5). All observations have been made from mature fertile fronds, and all characters of rachis, costa and lamina, unless otherwise noted, refer to the abaxial surface only.

The colors of the paleae, rachis, and costa are treated as black or one of the following three shades of red-brown. Because there is no satisfactory equivalent for the intermediate color, I have used the terms "light red-brown" (ferrugineous), "red-brown", and "dark red-brown" (castaneous).

As a result of the close morphological similarity of many of these species, it has been necessary to rely heavily on what may appear to be quite minute and technical characters. In evaluating the shape or comosity of paleae, or the size, shape, and distribution of hairs, it has often been necessary to use optical magnifications beyond the hand lens and up to 20 to 30 $\times$ or more.

The laminar trichomes consist basically of two types. One is the appressed, clavate, simple, forked, or ctenoid hair. These are rarely over 250 μ long and would be generally overlooked in routine identifications, except when they are conspicuous on the stipe base in the larger members of the *P. pectinatum* group. The second are conspicuous, acicular, simple hairs from 0.25 mm to 2.0 mm long. These constitute the generally visible pubescence of the frond. However, in the descrip-

tions both the conspicuous acicular hairs and the inconspicuous clavate hairs are referred to. Because the clavate hairs would often be overlooked, certain species may appear superficially glabrous, when in fact small clavate hairs are undoubtedly present. In these cases, the description may refer to the lamina as "essentially glabrous."

Where the soral size is important, it is indicated by the approximate portion of the width of the segment that two sori occupy, e.g. "occupying half the width of the segment." Only the mature sori are referred to in this measurement.

KEY TO THE SPECIES OF THE POLYPODIUM
PECTINATUM-PLUMULA COMPLEX

1. Rachis paleae relatively conspicuous, persistent, other than filiform; rachis brown or black.
 2. Rhizome paleae cordate with acute apex, non-comose; rachis red-brown or black with lateral brown stripes; rachis paleae narrow-elliptic or cordate with acute apex, entire; sporangia with or without setae.
 3. Rachis paleae narrow-elliptic, few and sometimes inconspicuous, flat; basal segments of the blade strongly reflexed; sporangia without setae; rachis red-brown or black with lateral brown stripes5. *P. alfredii*
 3. Rachis paleae cordate, numerous and conspicuous, bullate or flat; all segments perpendicular to the rachis, with symmetrical bases; sporangia with or without setae; rachis red-brown.
 4. Rhizome paleae light golden color; rachis red-brown but costa black or darker brown than the rachis; sporangia with 2 long setae6. *P. ferrugineum*
 4. Rhizome paleae red-brown; rachis and costa both red-brown; sporangia naked4. *P. cupreolepis*
 2. Rhizome paleae narrow-triangular with acuminate apex, comose; rachis red-brown or black without lateral stripes; rachis paleae cordate, or narrow-triangular with acuminate apex and hastate base, inconspicuously toothed or fimbriate; sporangia always setose, sometimes inconspicuously so.
 5. Fronds 10 (6-17) cm long; rachis paleae cordate, dark brown with dark base, inconspicuously toothed; veins unforked10. *P. filicula*
 5. Fronds 15-65 cm long; rachis paleae cordate or narrow-triangular and hastate, dark red-brown, lighter at the base, fimbriate; veins 1-2-forked.
 6. Fronds narrow-ovate or linear; segments linear, the basal segments shorter, not deflexed, reduced to mere auricles; veins 1-forked9. *P. plumula*
 6. Fronds narrow-ovate; segments narrow-ovate, the basal segments shorter, deflexed, sometimes reduced to auricles; veins 2-forked.
 7. Rachis and costa brown; Bermuda8. *P. bermudianum*
 7. Rachis and costa black; not from Bermuda.
 8. Rachis paleae subulate with hastate base; lower segments only slightly shortened, strongly deflexed; 64 reniform spores per sporangium; Central America12. *P. atrum*
 8. Rachis paleae narrow- to linear-triangular with hastate base; lower segments sometimes reduced to auricles, slightly deflexed; 32 globose spores per sporangium; wide-ranging11. *P. dispersum*
 1. Rachis paleae absent, or if present then filiform and inconspicuous; rachis brown.
 9. Basal segments one half as long as the longest segments or more.
 10. Fronds mostly less than 40 cm long; veins 1-forked26. *P. hygrometricum*
 10. Fronds mostly more than 40 cm long; veins 2- or 3-forked.
 11. Segments acuminate, gray-green, puberulent with short silvery hairs25. *P. recurvatum*
 11. Segments acute to obtuse, green, glabrous16. *P. bolivianum*

9. Basal segments less than half as long as the longest segments, often reduced to wings, lobes or auricles.
12. Veins simple; rhizome paleae glabrous.
 13. Segments ascending 15°-25° above the horizontal; segments 3.5 (2.5-4.5) mm wide; rhizome paleae brown to dark brown1. *P. truncorum*
 13. Segments perpendicular to the rachis or only slightly ascending; segments 1-2 mm wide; rhizome paleae light red-brown2. *P. siccum*
12. Veins 1-4-forked; rhizome paleae comose (except in *P. sursumcurrens*).
 14. Segments strongly ascending 25°-50° above the horizontal, crenulate to pinnatifid.
 15. Segments pinnatifid almost to the costa15. *P. choquetangense*
 15. Segments merely crenulate or crenate.
 16. Blades herbaceous; segments 2(1.5-3) mm wide; hairs of the rachis ca 1 mm long; apex of the blade usually circinate even at maturity14. *P. curvans*
 16. Blades coriaceous to herbaceous; segments 3.5(2-4.5) mm wide; hairs of the rachis ca 0.5 mm long; apex of the blade usually straight at maturity13. *P. absidatum*
14. Segments perpendicular to the rachis or only slightly ascending, entire to crenulate.
 17. Lamina pilose only in an oblong patch around the sorus, otherwise glabrous or with only scattered acicular hairs (then these much denser around the sorus); basal segments gradually reduced to mere wings or lobes23. *P. ptilodon*
 17. Lamina glabrous or with an even distribution of pubescence; segments at the blade base various.
 18. Lamina essentially glabrous beneath (acicular hairs absent or only scattered, inconspicuous clavate hairs present); veins free throughout.
 19. Lower edge of the segments perpendicular to the rachis, at least in the lower half of the blade; veins 1-forked.
 20. Spaces between segments 2-3 times the width of the segments; clavate hairs on the lamina numerous, short, blackish; sori submarginal to nearly marginal; receptacular paraphyses twisted and with a subterminal clavate multicellular head; eastern Mexico7. *P. sursumcurrens*
 20. Spaces between segments equal to or narrower than the segments; clavate hairs on the lamina few, golden and inconspicuous; sori medial to submarginal; receptacular paraphyses simple and straight.
 21. Rachis 2-3.5 times as long as the stipe; fronds 28-130 cm long; blade 4-26 cm wide17. *P. eurybasis*
 21. Rachis 4-14 times as long as the stipe; fronds 19-55 cm long; blade 3-7 cm wide.
 22. Rachis paleae linear; sori medial; rhizome paleae narrow-triangular, red-brown; northern Argentina and southern Brazil3. *P. singeri*
 22. Rachis paleae narrow-elliptic; sori medial to submarginal; rhizome paleae ovate to cordate, brown; Mexico and Central America5. *P. alfredii*
 19. Upper and lower edge of the segments similar, equally expanded and adnate on the rachis; veins 2-forked.
 23. Rachis 13 (6-20) times as long as the stipe; segments reduced at blade base to obtuse or rounded lobes, entire24. *P. consimile*
 23. Rachis 2-5 times as long as the stipe; segments reduced at the blade base but not to mere lobes, narrow-triangular, acute at the apex, crenulate or crenate17. *P. eurybasis*

- 18. Lamina pilose with acicular hairs (inconspicuous clavate hairs also present); veins free or partially anastomosing.
- 24. Lamina thinly pilose with long, conspicuous, blackish, clavate hairs; acicular hairs absent; sori submarginal or nearly marginal; veins 1-forked, free; rhizome paleae ovate, red-brown with dark brown base7. *P. sursumcurrens*
- 24. Lamina pilose with pale or golden and acicular hairs; sori medial to nearly marginal; veins 1- or 2-forked, free or partially anastomosing; rhizome paleae narrow- or linear-triangular, red-brown, lighter at the base.
- 25. Costa meeting the rachis at a perpendicular angle; veins free throughout; basal segments strongly deflexed; plants of Paraguay, Argentina, and southern Brazil.
- 26. Fronds less than 65 cm long; veins 1(2)-forked; sori supramedial; segments entire or occasionally crenulate20. *P. pectinatiforme*
- 26. Fronds over 70 cm long; veins 2- or 3-forked; sori submarginal; segments crenate21. *P. paradiseae*
- 25. Costa curved downward and decurrent on the rachis; veins free or partially anastomosing; basal segments various; wide-ranging.
- 27. Fronds less than 30 cm long; veins 1-forked, free throughout22d. *P. camptophyllum* var. *abbreviatum*
- 27. Fronds more than 30 cm long; veins 2(1)-forked, free or partially anastomosing.
- 28. Lamina chartaceous-herbaceous, soft; veins rarely anastomosing; sporangia without setae; Peru and northern Argentina19. *P. venturii*
- 28. Lamina herbaceous-coriaceous, firm; veins always at least partially anastomosing; sporangia setose; wide-ranging.
- 29. Lamina puberulent with hairs usually much shorter than 0.2 mm long; sporangial setae ca 65 μ long; segments usually abruptly reduced to 2 or 3 pairs of lobes at the blade base, perpendicular to the rachis throughout, the basal lobes expanded and symmetrical at the base18. *P. pectinatum*
- 29. Lamina pubescent with hairs 0.35 to 0.5 mm long; sporangial setae more than 100 μ long; segments reduced to lobes, or reduced, deflexed and abruptly terminated, the basal segments subsymmetrical at the base or with the lower edge perpendicular to the rachis22. *P. camptophyllum*

1. *Polypodium truncorum* Lindm., Hedwigia 43: 309, 1904.

P. elasticum Rich. var. *glaziovii* Baker in Mart., Fl. Bras. 1(2):517, t. 64, fig. 2., 1870.
(Syntypes: Brazil: Santa Catarina, Muller s.n. not seen; Rio de Janeiro, Glaziou 1723, 2461 not seen; Minas Gerais, Caldas, Regnell II 319* MO)

P. bakeri Lindm., Ark. Bot. 1: 240, t. 11, fig. 9, 1903, non Luer, 1882. (Lectotype: Brazil, Minas Gerais, Caldas, Pedra Branca, Regnell II 319*a S; isotype S-PA)

Ctenopteris glaziovii sensu Copel., Phil. Jour. Sci. 84: 416, 1956, p.p., not as to type.

C. truncorum (Lindm.) Copel., loc. cit. 450.

Rhizomes very short-creeping or erect, 1.5 (1-2) mm in diam; rhizome paleae narrow-triangular, brown to dark brown, lustrous, basifixed, non-comose, non-clathrate, the margins entire; *fronds* 25 (8-42) cm long, caespitose on the rhizome; rachis 9 (6-20) times as long as the stipe; stipe and rachis red-brown, with scattered whitish or golden acicular hairs, ctenoid hairs absent; rachis paleae inconspicuous or absent, if present then linear to short-filiform, entire; *blades* narrow- to linear-ovate or -obovate, 23 (7-38) cm long, 3.5 (2.5-4.5) cm wide, subtruncate to cuneate at the base; segments 19 (13-23) mm long, 3.5 (2.5-4.5) mm wide, narrow-triangular, acute, expanded and symmetrical at the base, chartaceous to membranaceous, slightly toothed, ascending ca 65°-75° from the rachis, slightly reduced but not deflexed at the blade base, the basal pair usually reduced to auricles, or occasionally blades gradually reduced to a cuneate base; lamina essentially glabrous except for a few long, clavate hairs; costae perpendicular to or slightly ascending on the rachis, with few long acicular hairs; veins simple, free; guard cells ca 41 μ long; sori medial to extramedial, round, with long simple clavate paraphyses; *sporangia* without setae; spores globose-reniform, smooth, ca 45 μ long.

Type: Based on *P. bakeri* Lindm., 1903, not Luer., 1882. Regnell's numbering system was complex; *II 319a*, *II 319**, *II 319*c* and *II 319*d* have been examined and they represent other species, the two last named numbers being *P. singeri*.

Habitat: epiphytic, mostly on tree-fern trunks, occasionally terrestrial, in wet forests, 500-1800 m alt.

Distribution: southern Brazil and northern Argentina.—Fig. 11.

BRAZIL: MINAS GERAIS: Canjerana, Regnell *II 319** p.p. (MO, non US); Caldas, Regnell *II 319*b* (S-PA); Carangola, N of Serra da Gramma, Mexia 4272 (GH); Viçosa, Fazenda de Aguada, Mexia 5105 (GH). RIO DE JANEIRO: Tijuca, Dusén 5022 (MO); nr Rio de Janeiro & Bahia, Webb s.n., in 1867-1868 (MICH). SAO PAULO: Alto da Serra, Estação Biológica, Smith 1844 (MICH); Campos do Jordão, Leite 3562 (GH, MO); Serra da Bocaina, Brade 20799 (MO), 20801 (MO); Serra da Cantareira, Eiten & de la Sota 2170 (US). PARANA: Serra do Mar, Ypiranga, Dusén 3651 (GH, MO); Desiro Ypiranga, Dusén 6776 (MO). SANTA CATARINA: Ararangua, Serra da Pedra, Reitz C271 (US); Azambuja, Brusque, Reitz 1795 (US), Smith & Reitz 6136 (GH, MO); Brusque, Mata Hoffmann, Reitz 3071 (US); Ibirama, Horto Florestal, Smith & Klein 7554 (US); Itacorobi, Santa Catarina I, Rohr 320 (US); Luis Alves, Itajai, Reitz 159 (US). RIO GRANDE DO SUL: São Leopoldo, Reitz 1314 (US).

ARGENTINA: MISIONES: Yermal Viejo, Burkart 1584 (GH); Cainguás, Qae Mayo, Montes 27.218 (US).

I have not seen the type of *P. glaziovii* Bak. (Glaziou 9062, presumably at BM or P), which I believe to be a *Ctenopteris*. Copeland (1956) transferred *P. glaziovii* Bak. to *Ctenopteris*, using Baker's original description and citing the type specimen, but in a way indicating that he had not seen it. He then stated, "I find the veins simple; the spores tetrahedral, the stipes glabrescent," and cited eight collections. I have examined five of these collections. The spores of these are not tetrahedral. The veins are simple, as Copeland stated, but this alone is insufficient for separation of *Ctenopteris* and *Polypodium* in all cases. The stipes are glabrescent, but with polypodioid articulate hairs and not ctenopteroid unicellular setiform hairs. These five sheets are all *P. truncorum*. It is evident thus that Copeland had a confused concept of his *Ctenopteris glaziovii* (Baker) Copel.; the type may be a true

Ctenopteris, but at least five of the collections cited by Copeland belong to *Polypodium*.

This species is very similar to *P. siccum*, from which it can be distinguished by the very small rhizome with crowded stipes, the dark chestnut rhizome scales, membranous frond texture, and the narrow ascending segments with the basal pair reduced to mere auricles and the next pair only slightly reduced. That it is a true *Polypodium* and not a *Ctenopteris* was shown by de la Sota (1963).

2. *Polypodium siccum* Lindm., Ark. Bot. 1: 234, t. 11, fig. 4, 1903.

P. heteroclitum Fée, Crypt. Vasc. Bras. 1: 93, t. 26, fig. 4, 1869, non Desv., 1811 (Type: Brazil, Rio de Janeiro, Glaziou 2410 BR, C, P)

Rhizomes short-creeping to erect, 2 (1-3) mm in diam; rhizome paleae narrow-triangular, light red-brown, basifixed, non-comose, non-clathrate, entire; *fronds* 27 (10-50) cm long, caespitose on the rhizome; rachis 8 (4.5-11) times as long as the stipe; stipe and rachis red-brown, pilose with long acicular simple hairs, and also with long clavate hairs, ctenoid hairs absent; rachis paleae inconspicuous or absent, if present then linear to filiform, light red-brown, entire; *blades* linear to narrow-ovate, 23 (8-36) cm long, 3 (2-5) cm wide, cuneate to narrow-cuneate, occasionally subtruncate at the base; segments 15 (9-22) mm long, 1.5 (1-2) mm wide, perpendicular to the rachis, reduced to a narrow wing at the blade base, linear-triangular, chartaceous to herbaceous, acute, slightly toothed, expanded and symmetrical at the base, or with the lower edge perpendicular to the rachis in the lower part of the blade, the sinuses approximately equal to the width of the segment; lamina with numerous long golden clavate hairs; costa decurrent on the rachis, with scattered long acicular hairs; veins simple, free; guard cells ca 37μ long; sori submarginal, round, with simple clavate paraphyses, ca 0.3 mm long; *sporangia* without paraphyses; spores globose-reniform, smooth, ca 45μ long; $n=37$.

Lectotype: Brazil, Rio de Janeiro, Glaziou 3339 S; isoelectotypes BR, C, S-PA. Syntypes: Brazil, Cañas, Rio Grande do Sul, Regnell I A391 G, GH, NY, S, S-PA, US; Brazil, Hamberger Berg, Rio Grande do Sul, Regnell I A501 S, S-PA; Paraguay, Cordillera of Villa Rica, Balansa 667 B, BR, G, S-PA.

Habitat: epiphytic, often on tree ferns, in forests, 450-1200 m alt.

Distribution: southeastern Brazil, Paraguay and northern Argentina.—Fig. 10.

BRAZIL: RIO DE JANEIRO: Novo Friburgo, Dusén 1899 (US), Leite 4104 (MO); Rio de Janeiro & Teresópolis, Clarke s.n. (US); Santo Antonio, Serro dos Orgãos, Brade 16317 (MO). SAO PAULO: Iguape, Rio Peronpaua, Brade 7737 (US); Morro das Pedras, Brade s.n., in 1918 (US). PARANÁ: Lapa, Braga 1041 (US); Serra do Mar, Ypiranga, Dusén 14433 (GH, MO); Villa Velha, Dusén 14813 (US); Volta Grande, Dusén 14141 (US). SANTA CATARINA: Mun. Curitibanos & Campos Novos, Smith & Klein 8287 (US); Joinville, Schmalz 59VIII (MO); Lages, Spannagel 67 (US); Mun. Pôrto União, Smith & Reitz 8672 (US). RIO GRANDE DO SUL: Cañas, Regnell IA391 (G, GH, NY, S, S-PA, US); Neu-Wurtemberg, Bornmüller 120 (GH); São Leopoldo, Anchieta 2664 (US), Chacara Meyer, Reitz 161 (US); Regnell IA501 (S, S-PA).

PARAGUAY: E of the Vilarica Mts, Balansa 667 (B, BR, G, S-PA).

ARGENTINA: CORRIENTES: General Paz, Paraje Angostura, Ibarrola 3819 (MO); Mburucuyá, Santa Teresa, Petersen 1758 (MO, US). MISIONES: Loreto, Burkart 1551 (GH); Posadas, Bonpland, Ekman 66 (MO).

This species is best recognized by its long, linear, delicate blades, submarginal sori, and bright ferruginous rhizome paleae. Within its range, the only similar species is *P. truncorum*, which has, however, much wider segments and darker paleae. *Polypodium siccum* (like *P. truncorum*) strongly resembles the ctenopteroid ferns, but in the critical characters of spores, sporangial stalks, and paleae, it is properly placed in *Polypodium*.

One specimen indicates that this species reproduces in part by root proliferations, though apparently not so commonly as in *P. dispersum* or *P. filicula*.

3. *Polypodium singeri* de la Sota, Opera Lilloana 5: 181, 1960.

P. pectinatum L. var. *aurita* Rosenst., Hedwigia 46: 138, 1906, non *P. auritum* Lowe, 1858. (Holotype: Brazil, Lages, Spannagel 116a S-PA)

P. pectinatiforme Lindm., loc. cit. 43: 309, 1904, p.p., not as to lectotype.

Rhizomes short-creeping, 3 (2-4) mm in diam; rhizome paleae narrow-triangular, red-brown, lustrous, basifixed, acuminate, non-comose, non-clathrate, entire; *fronds* 25 (19-30) cm long, caespitose; rachis 6 (3-8) times as long as the stipe; stipe and rachis red-brown, with scattered golden, acicular hairs, ctenoid hairs absent; rachis paleae inconspicuous, red-brown, linear, entire; *blades* narrow-ovate, 22 (15-27) cm long, 4.3 (3-6) cm wide, cuneate at the base; segments 22 (15-25) mm long, 3 (2.5-3.5) mm wide, perpendicular to the rachis, strongly deflexed at the blade base or reduced to auricles, linear-ovate, obtuse at the apex, asymmetrical at the base with the upper edge widely adnate on the rachis and the lower edge perpendicular to the rachis or incised, occasionally auriculate, chartaceous, entire, the sinuses equal to or narrower than the segments; lamina essentially glabrous except for scattered clavate, simple hairs; costa perpendicular to the rachis, with scattered, golden, acicular hairs; veins simple or once-forked, free; sori medial, round, with simple clavate paraphyses; *sporangia* without setae or with one capsular seta ca 115 μ long; spores reniform, slightly tuberculate, ca 32 μ long.

Holotype: Argentina, Misiones, San Ignacio, Loreto, 2 Febr 1958, Cristóbal, Ahumada, & de la Sota 53 LIL, not seen; isotypes BR, S, US.

Habitat: epiphytic on very small tree stems and tree-fern trunks, occasionally terrestrial, in humid forest, 700-1200 m alt.

Distribution: southeastern Brazil to northern Argentina.—Fig. 8.

BRAZIL: MINAS GERAIS: Caldas, Regnell II 319* p.p. (US, non MO), II 319*c (S), II 319*d (S); Passa-quatro, Brade 19006 (MO). SAO PAULO: Campinas, Heiner 504 (S), 616 (S-PA). PARANA: Jaguariahyva, Dusén 14880 (GH, MO); Rio Negro, Annies (Rosenstock 113) (US); Villa Nova, Annies (Rosenstock 113) (S, S-PA, US); Vierdel 1* (S-PA). SANTA CATARINA: São Carlos, Chapeco, Reitz 3769 (US). RIO GRANDE DO SUL: Silveira Martins, Santa Maria, Pivetta 158 (US); Serra Leitão, Jürgens 105 (S); Santa Cruz, Jürgens s.n. (Rosenstock 113) (US), (Rosenstock 113a) (S-PA); Regnell 750 (S).

ARGENTINA: MISIONES: Candelaria, La Pastora, Montes 2340 (MO); Loreto, Moreau s.n., 27 July 1931 (GH); San Ignacio, Montes 2249 (GH); Posados, Bonpland, Lilliesköld s.n. (S), Ekman 67 (S, S-PA), 81 (S).

This species has a curious habit due to its vegetative reproduction by root proliferation. It is usually found growing on small upright twigs as a series of short interconnected rhizomes. The whole appears as a layer of roots surrounding small stems with a series of short rhizomes imbedded in the root mass. The species

is well characterized by this curious serial arrangement of rhizome, the conspicuously asymmetrical and glabrous segments, the small size of the frond, and the non-comose rhizome scales. It is apparently closely related to *P. alfredii* of Central America, although well separated by the broader blade, more asymmetrical segments, and the longer rachis paleae.

Within this species there appear to be two variations. One form has the segments with smooth entire margins and the sporangia generally without setae, while the other tends to have slightly undulate margins and one seta on most of the capsules. The plants are alike in all other respects, however, so that unless careful population studies in the future indicate otherwise, I believe them to be taxonomically inconsequential. Rosenstock based his *P. pectinatum* var. *aurita* on a leaf form with narrow excurrent auricles on the lower edge of the segment.

4. *Polypodium cupreolepis* A. M. Evans, sp. nov.—Fig. 17.

Rhizoma breviter repens, paleis ovatis vel cordatis, pallide vel fusco-brunneis, non comosis, integris, basi affixis, apice acutis, cellulis non clathratis; frondes approximatae articulatae, ca 30 cm longae; stipites et rhachides rigidae nitentes brunneae, pilose dissitos ferentes; paleae rhachidis numerosae conspicae cordatae, aureae vel ferrugineae, integrae, apice acutae; lamina pectinata anguste ovata, ca 22 cm longa et 4 cm lata, basi abrupte cuneata vel subtruncata; segmenta linearia integra, rhachide perpendicularia vel interdum basalia paullo deflexa; lamina solum cum pilis inconspicuis clavatis; venae liberae, 1-furcatae; sporangia sine setis; sporae late reniformes laeves, ca 36 μ longae.

Rhizomes short-creeping 4.5 (3-7) mm in diam; rhizome paleae ovate to cordate, pale to dark brown, non-lustrous, basifixed or basally cordate, acute, non-comose or rarely inconspicuously comose, entire; *fronds* 30 (10-60) cm long, approximate on the rhizome; rachis 3 (1.5-5) times as long as the stipe; stipe and rachis brown, with long, scattered, acicular hairs; rachis paleae numerous, conspicuous; broadly cordate, bullate, acute, basifixed, golden to light red-brown, non-lustrous, entire; *blades* narrow-ovate, 22 (9-47) cm long, 4 (2.5-6.5) cm wide, abruptly cuneate to subtruncate at the base; segments 20 (12-32) mm long, 2.5 (1.5-3) mm wide, perpendicular to the rachis, or occasionally slightly ascending in the upper part of the blade, strongly reduced and sometimes deflexed at the blade base, herbaceous, obtuse to acute at the apex, subsymmetrical at the base or the lower edge perpendicular to the rachis, entire; lamina essentially glabrous, but with inconspicuous clavate hairs; costa decurrent on the rachis, with scattered acicular hairs; veins once-forked, free; guard cells ca 31 μ long; sori medial, round, with numerous, long, clavate paraphyses; *sporangia* without setae; spores broadly reniform, smooth, ca 36 μ long.

Holotype: Mexico, Michoacán, hills of Patzcuaro, 8 Nov 1890, *Pringle* 3353 US; isotypes, B, GH, MICH, MO, US.

Habitat: epiphytic or epipetric, occasionally terrestrial, in montane forests, 1100-2900 m alt.

Distribution: western and southern Mexico to Costa Rica.—Fig. 10.

MEXICO: SINALOA: betw Durango & Villa Unión, Ownbey 1939 (US); Ocurahui, Sierra Surutato, Gentry 6337 (GH, MO). DURANGO: 22 mi E of Santa Lucía, rd from Villa Unión to Durango, Reeder 2487 (US). JALISCO: 15 mi SSE of Autlán, Wilbur 1927 (US); below Canoa de Leoncito, McVaugh 13486 (US); Santa Mónica, McVaugh 14042 (US); 7 mi SSW of Tecalitlán, McVaugh 16254 (US). HIDALGO: Trinidad, Pringle 13475 (US). PUEBLA: Ixtaccihuatl, Purpus 1828 (GH, MO, US). MORELOS: Valle del Tepeite, Lyonnet 779 (MO). DISTRITO FEDERAL: Eslava, Lyonnet 3315 (US), 3316 (US). MICHOACÁN: Morelia, Campanario, Arsène 8464 (GH, MO, US); Cerro Azul, nr Morelia, Arsène, 3 May 1910 (GH); Tancitaro, Uruapán, Hinton et al. 15478 (GH, MO, US); Tancitaro, Leavenworth 336 (GH), 516a (GH), Mt San Miguel, Leavenworth & Hoogstraal 1097 (MO); Zitácuaro, Zitácuaro-Cacique, Hinton 13178 (GH, MO, US). COLIMA: Volcán Colima, Goldsmith 40 (GH); Revillagigedo Islands, Socorro I, Mason 1633 (GH). GUERRERO: Omilteme, Rowell 3049A (US); 2 mi W of Omilteme, Hamilton & Rowell 3245 (US). OAXACA: Totontepec, Nelson 796 (US). CHIAPAS: Pico de Loro, nr Escuintla, Matuda 4268 (GH).

GUATEMALA: ALTA VERAPAZ: Cobán, von Tuerckheim 645 (US). QUEZALTENANGO: Cerro Quemado, Kellerman 5940 (US). CHIMALTENANGO: Las Calderas, Standley 60040 (US). ESCUINTLA: Volcán de Fuego, Salvin s.n. (GH).

EL SALVADOR: SANTA ANA: NE of Cerro del Aguila, Tucker 1249 (US). SAN VICENTE: Volcán de San Vicente, Standley 21609 (US).

NICARAGUA: JINOTEGA: Jinotega, Howard 79 (US).

COSTA RICA: SAN JOSÉ: Las Nubes, Scamman 7228 (GH).

This species has generally been identified as "*P. pulchrum*," the type of which has, however, a black rachis and costa, triangular, lustrous, red-brown rhizome scales, setose sporangia, and somewhat different rachis scales. I consider *P. pulchrum* a synonym of *P. plumula* Humb. & Bonpl. *Polypodium ferrugineum* Mart. & Gal., a smaller plant with two setae per sporangium, a black costa, a brown rachis, and much paler golden-tan rhizome scales, appears to be its nearest relative.

The isotype at Berlin has been annotated by Hieronymus as "*P. patzcuarensis*," which seems to be an unpublished name.

5. *Polypodium alfredii* Rosenst., Repert. Sp. Nov. **22**: 15, 1925.

P. alfredii var. *curtii* Rosenst., loc. cit. (Holotype: Costa Rica, region of Río Chris, nr Juan Vinas, 1200 m, Brade 695 S-PA; isotype US)

P. tablazianum Rosenst., loc. cit. 14. (Lectotype: Costa Rica, Tablazo, 1800 m, 4 Mar. 1908, Brade & Brade 14 S-PA. Syntypes: Costa Rica, Tablazo, 1900 m, 20 July 1909, Brade & Brade 696 NY; Costa Rica, Carpintera, 1500 m, 14 Dec 1909, Brade & Brade 149 NY, S-PA, US)

P. cyathicola Copel., Univ. Calif. Publ. Bot. **19**: 292, t. 43, 1941. (Holotype: Mexico, Veracruz, Cuantlancillo (Orizaba) alt 1600 m, on *Cyathea* in wet ravine, 1 Mar 1938, Copeland, Mex. Ferns 127 MICH; isotype US)

Rhizomes short-creeping, 4 (3-5) mm in diam; rhizome paleae brown, non-lustrous, ovate to cordate, acute to rounded, basifixed, entire or rarely irregularly fimbriate toward the apex; *fronds* 36 (20-55) cm long, fasciculate on the rhizome; rachis 7.5 (4-14) times as long as the stipe; stipe and rachis red-brown, or black with lateral brown stripes, with scattered, long, acicular hairs, ctenoid hairs absent or few and inconspicuous; rachis paleae brown, non-lustrous, acute, basifixed, entire; bullate-cordate to narrow-ovate and conspicuous, or narrow-ovate to narrow-obovate, inconspicuous and scattered, *blades* 31 (20-50) cm long, 4.8 (3.3-7) cm wide, narrowly oblong, cuneate at the base or subtruncate with the lower segments strongly deflexed, sometimes parallel to the stipe; segments linear-triangular to

linear, acute, 25 (15-35) mm long, 3 (2-3.5) mm wide, symmetrical at the base in the upper half of the frond, the lower edge perpendicular to the rachis or deflexed in the lower half of the frond, ciliate, entire; lamina chartaceous, with scattered, short, clavate hairs; costa brown, occasionally darker than the rachis, with scattered, long, acicular hairs, slightly decurrent on, or perpendicular to, the rachis; veins once-forked, free; guard cells ca 35μ long; sori submarginal to extramedial, round, with numerous long, clavate paraphyses; *sporangia* without setae; spores reniform, smooth, ca 49μ long; $n = 37$.

Holotype: Costa Rica, Turrialba, 650 m, 5 Aug 1909, *Brade & Brade* 697 S-PA; isotype US.

Habitat: epipetric or epiphytic on tree trunks, 1220-2500 m alt in ravines and mountain forests.

Distribution: southeastern Mexico to Costa Rica.—Fig. 10.

MEXICO: HIDALGO: Chapulhuacán, *Sharp* 441768 (TENN, US); nr Jacala, *Knobloch* 718 (US). VERACRUZ: Cuantlancillo, *Copeland* 127 (GH); summit of El Cerro de Ejecatepetl, *Santos* 2990 (MICH, US); nr El Puerto, above Acultzingo, *Sharp* 44822 (US); Jalapa, *Orcutt* 2819 (MO, US), *Smith* 2219 (GH, MO); Orizaba, *Mohr s.n.*, in 1857 (US), *Mohr & Botteri s.n.*, in Sept, 1857 (US); Orizaba to Tzhuatlanchilla, *Bourgeau* 2609 (GH, US). PUEBLA: summit of El Cerro de Cuhuatepetl Tehuacán, *Santos* 3678 (MICH, US). MORELOS: Valle del Tepeite, *Lyonnet* 779 (GH). OAXACA: Cuicatlán, Cuyamecalco, *Conzatti & Gómer* 3499 (US). CHIAPAS: Los Lagos, SE of Comitán, *Carlson* 1777 (US); Pico de Loro, *Matuda* 4268 (MO); San Felipe, nr Ciudad las Casas, *Carlson* 1615 (US); San Pablo, *Münch* 121 (US); *Ghiesbreght* 262 (GH).

GUATEMALA: ALTA VERAPAZ: Santa Cruz, *Johnson* 980 (US). CHIMALTENANGO: Tecpán, *Skutch* 572 (US).

HONDURAS: COMAYAGUA: El Achote, above Siguatepeque, *Yuncker et al.* 6191 (US); nr El Rincón, *Yuncker et al.* 6076 (GH, MO, US); Barranco El Socorro, *Williams & Williams* 18377 (US). FRANCISCO MOROZÁN: Cerro de Uyuca, *Morton* 6914 (US), 6975 (US); betw La Branza & Las Flores, *Molina R.* 1107 (US), 1298 (US); betw Peña Blanca & Lo de Ponce, *Williams & Molina R.* 17128 (US).

COSTA RICA: GUANACASTE: nr Tilarán, *Standley & Valerio* 44666, 44713, 44757 (US). ALAJUELA: Alajuela, *Alfaro* 6056 (GH, US). SAN JOSÉ: Tablazo, *Brade & Brade* 696 (NY), 14a (S-PA). CARTAGO: Cervantes & Padayas, *Biolley* 95 (US); El Muñeco, *Stork* 4708 (US); Juan Viñas, Reventazón Valley, *Cook & Doyle* 204 (US), 242 (US); Orosi, *Scamman* 6117 (GH); Pejivalle, *Skutch* 4625 (GH, MO); Peralta, *Rowlee & Rowlee* 60 (US); Tuis, *Tonduz* 11309 (US); Turrialba, *Scamman* 6116 (GH), 6121 (GH, US), 7230 (GH, US), 7765 (GH); Río Turrialba, *Smith* 5091 (US).

There are two extreme types. Typical northern material (represented by *Copeland's P. cyathicola*) has either a long-cuneate frond base and a short stipe, or subtruncate and strongly deflexed segments at the blade base, a black rachis with lateral brown stripes, and inconspicuous narrow-ovate rachis scales. The typical southern material represented by *P. tablazianum* and *P. alfredii* has a brown rachis and conspicuous, cordate rachis scales. However, these characters are less consistent than the entire, dark brown rhizome scales, the linear-triangular chartaceous segments, and the extra-medial sorus position. The rachis scales throughout the *P. pectinatum-plumula* complex show patterns of consistency in some and inconsistency in other species. *Polypodium plumula* (see Fig. 5) has a clinal variation of rachis scales. The rachis scales of *P. dispersum* and *P. atrum* are very similar (more similar than the range of variation in *P. plumula*) but because of other

over-riding characters, these species warrant recognition. In *P. alfredii* (as here construed) both the cordate and lanceolate scales can be found on any one frond except on those plants from Mexico where the broader scales are completely lost.

6. *Polypodium ferrugineum* Mart. & Gal., Mém. Acad. Bruxelles **15**: 36, t. 6, fig. 2, 1842.

Rhizomes short-creeping, 3.5 (2-5) mm in diam; rhizome paleae broad-ovate to cordate, golden-tan, basifixed, acute, non-clathrate, non-comose, the margins entire; *fronds* 20 (8-40) cm long, approximate to fasciculate on the rhizome; rachis light red-brown, thinly pilose with long, harsh, acicular hairs, and also with clavate hairs, ctenoid hairs absent; rachis paleae scattered, inconspicuous, linear-ovate to -obovate, light red-brown, obtuse to acute, entire; *blades* narrow-ovate, 17 (9-35) cm long, 4 (2-6.5) cm wide, cuneate to subtruncate at the base; segments 20 (10-32) mm long, 2.5 (1.5-3) mm wide, linear to narrow-ovate, perpendicular to the rachis except the strongly deflexed ones at the blade base, herbaceous, acute, the base expanded and symmetrical in the top half of the frond, subsymmetrical or with the lower edge perpendicular to the rachis in the lower half of the blade, entire; lamina with scattered clavate hairs, and occasional acicular hairs; costa decurrent on the rachis, dark red-brown or blackish, with scattered, long, acicular hairs, without paleae; veins once-forked, free; guard cells ca 40 μ long; sori medial, round, with simple, clavate paraphyses; *sporangia* with 3 (2-4) capsular setae, 70-120 μ long; spores globose reniform, smooth, ca 50 μ long; $n = 37$.

Holotype: Mexico, Oaxaca, forests of Zacatepèque and Juquila, *Galeotti* 6354 BR not seen, fragment US.

Habitat: epipetric, rarely epiphytic, from canyons, cliffs and river banks, 500-2100 m alt.

Distribution: western Mexico.—Fig. 8.

MEXICO: SINALOA: Colomas, *Rose* 3201 (US); Panuco, *Pennell* 20010 (US); Paraje del Zapote, *Salazar* 393 (US); Sierra Monterey, *Gentry* 5883 (GH, MO, US). NAYARIT: Ceboruco volcano, *Mickel* 1374 (EVANS); La Atarjea, N of Yxtlán, *Mexía* 880 (GH, MO, US); Santa María del Oro, *Pennell* 19868 (US); Cerro de San Juan, *Mexía* 690 (GH); E of Jalcocotán, rd to Tepic, *McVaugh* 13342 (US). JALISCO: E of Mamantlán, S-SE of Autlán, *Wilbur* 1969 (US); Pihuamo, *Jones* 511 (MO, US). HIDALGO: Hidalgo, km 330, *Herb. Copeland* 16056 (MICH). MORELOS: Cuernavaca, *Kenoyer* 40 (US), *Rose & Painter* 6870 (GH, US); Teposteco, *Lyonnet* 2583 (US); Ramanoa Teatzalán, nr Tepoztlán, *Seler* 4516 (GH); Tepoztlán, *Herb. Copeland* 125 (GH, MICH, US); Valle del Tepeite, *Lyonnet* 779 (US). MEXICO: Temascaltepec, Ypericones, *Hinton* 4161 (GH). COLIMA: Revillagigedo I, Socorro I, *Barkew* 236 p.p. (US). GUERRERO: Mina, *Manchon*, *Hinton* 9607 (MICH); Mazatlán, *Correll* 14391 (US). OAXACA: Cerro de San Felipe, *Conzatti & González* 334 (GH). CHIAPAS: Ixtape, *Münch* 12 (US).

This central and southern Mexican species is distinctive in its small size, light brown rachis and darker costa, long-setose sporangia, light brown rachis scales, and golden, ovate rhizome scales. Although this species has usually been identified as *P. plumula*, its nearest relatives are *P. cupreolepis* and *P. alfredii*, and it combines certain of the characters of each. It has normal appearing spores and is a diploid, so it is probably not of hybrid origin.

7. *Polypodium sursumcurrens* Copel., Univ. Calif. Publ. Bot. **19**: 291, t. 42, 1941.

Rhizomes short-creeping, 4 (3-5) mm in diam; rhizome paleae ovate to broad-ovate, red-brown at the margins with dark brown center, lustrous, basifixed or cordate, acute to obtuse, occasionally inconspicuously comose, non-clathrate, entire; *fronds* 30 (12-65) cm long, fasciculate on the rhizome; rachis 4 (2.5-6) times as long as the stipe; stipe and rachis red-brown, thinly pilose with blackish hairs up to 1 mm long, without ctenoid hairs; rachis paleae absent; *blades* narrow-ovate, 25 (10-56) cm long, 5.5 (3.5-8.5) cm wide, cuneate at the base; segments 28 (18-44) mm long, 3 (2-4) mm wide, perpendicular to the rachis, reduced and slightly deflexed at the blade base with the lowest 2 or 3 pairs reduced to auricles, linear-triangular, acute, asymmetrical at the base with the lower edge perpendicular to the rachis throughout the blade, herbaceous, entire to crenulate, the spaces between the segments 2 to 3 times the width of the segments; lamina with numerous blackish, simple, clavate hairs up to 175μ long; costa perpendicular to, or slightly decurrent on, the rachis, with scattered, long, acicular hairs; veins once-forked, free, guard cells ca 38μ long; sori marginal to submarginal, round, with numerous twisted paraphyses with a multicellular irregular clavate head, ca 375μ long; *sporangia* without setae; spores globose-reniform, smooth, thick-walled, ca 49μ long.

Holotype: Mexico, Veracruz, mountain tops at head of Orizaba Valley, 2400 m, epiphyte in mossy woods, *Copeland, Mexican Ferns* 128 MICH; isotypes GH, US.

Habitat: epiphyte in montane forests, 2400-2600 m alt.

Distribution (Fig. 9): MEXICO: VERACRUZ: El Puerto, *Sharp* 44822 (US). PUEBLA: Honey Station, *Pringle* 13475 (MICH).—Fig. 9.

This species is a narrow endemic in eastern Mexico. I have seen only two collections in addition to the type. Copeland mentions the distinctive feature of the blackish hairs of the lamina. However, they are the usual golden color but are uniformly attacked by a pyrenomycete fungus, which gives them this characteristic blackish appearance.

The relationships of this species are not obvious, though it is clearly in the *P. plumula* group. It is probably closest to *P. alfredii*, *P. ferrugineum*, and *P. cupreolepis*, from which it differs in the larger size, more widely spaced segments, especially in the larger fronds, the gray-green color, long rachis hairs, dark brown, ovate rhizome paleae, the lack of rachis paleae, and especially the unique paraphyses.

8. *Polypodium bermudianum* A. M. Evans, sp. nov.—Fig. 17.

P. pectinatum var. *squamosum* Lindm., Ark. Bot. **1**: 238, 1903, p.p., as to Bermuda, *Herb. Farlow* (GH), not as to lectotype. (See *P. dispersum*).

Rhizoma breviter repens, paleis anguste ovatis, castaneis, non comosis, inconspicue dentatis, basi affixis, apice acuminatis; frondes approximatae articulatae, ca 35 cm longae; stipites et rhachides rigidae nitentes castaneae, sparse pilosae; paleae rhachidis numerosae parvae, anguste triangulares, castaneae, basi hastatae, apice acuminatae; lamina pectinata, anguste ovata, ca 25 cm longa et 7 cm lata, basi abrupte cuneata; segmenta anguste ovata, ca 35 mm longa et 4-5 mm lata, rhachide perpendicularia, apice obtusa, basi symmetrica; lamina solum cum pilos brevibus

clavatis; venae liberae 1-furcatae; sporangia cum saepe 2-capsularibus setis; spora globoso-reniformes, paullo tuberculatae, ca 43μ longae, 64 per sporangium.

Rhizome short-creeping, 5 (4-7) mm in diam; rhizome paleae narrow-ovate, red-brown, acuminate, non-comose, basifixed, non-clathrate, inconspicuously toothed; *fronds* 35 (15-55) cm long, approximate on the rhizome; rachis 3 (2.5-4) times as long as the stipe; stipe and rachis red-brown, pilose with long, simple, acicular hairs, ctenoid hairs absent; rachis paleae conspicuous, red-brown, paler at the base, narrowly triangular, hastate at the base, acuminate, occasionally toothed; *blades* narrow-ovate, 25 (14-33) cm long, 6.8 (5.7-8.5) cm wide, abruptly cuneate at the base; segments 35 (28-44) mm long, 4-5 mm wide, perpendicular to the rachis, slightly reduced or auriculate at the base of the blade, herbaceous, obtuse, symmetrical at the base, entire, the spaces between the segments equaling the width of the segments; lamina essentially glabrous, with short, clavate hairs; costa decurrent on the rachis, pilose with acicular hairs, with reduced paleae similar to those of the rachis; veins once-forked, free; guard cells ca 43μ long; sori medial, round, with simple clavate paraphyses; *sporangia* mostly with 2 two-celled capsular setae, 130-175 μ long; spores globose-reniform, slightly tuberculate, ca 43μ long.

Holotype: Bermuda, Tuckers Town, on rocks, 10 Febr-9 Mar 1908, *Brown* 464 US 848332; isotype GH.

Habitat: on limestone rocks in lime-sink areas.

Distribution: BERMUDA: *Goode s.n.*, Mar, 1877 (MO), Apr, 1877 (US); *Goode s.n.* (US); *Reinwardt s.n.* (GH). HAMILTON ISLAND: Walsingham, *Harshberger s.n.*, June 1905 (GH, US); Walsingham Caves, *Moore 3118a* (GH), *Taylor 49-1163* (MICH); Paynter Vale, *Farlow s.n.*, June 1881 (GH), *Britton & Brown 267* (US).

This species can be distinguished from *P. plumula* by the brown rachis and the broad segments, and from *P. ptilodon* var. *caespitosum* by the once-forked veins and the rachis scales. It is distinguished from *P. dispersum* by the number of spores per sporangium and the brown rachis. Of the sexual species, it is probably closest to *P. atrum*, from which it can be distinguished by its brown rachis, once-forked veins, basal segments not deflexed, and the costa being decurrent on the rachis. Its close similarity to *P. atrum* and *P. dispersum* indicates its affinities to these two species. The problem of specific and varietal rank in these three species is complicated by the unique life cycle of *P. dispersum*, which demands its separation. I have, therefore, accorded specific rank to this narrowly confined endemic.

9. *Polypodium plumula* Humb. & Bonpl. ex Willd. in L., Sp. Pl., ed. 4, 5: 178, 1810.

P. schkuhrii Raddi, Opusc. Sci. Bol. 3: 287, 1819. (as "Schkuhri"). Pl. Bras. 1: 19, t. 27, fig. 2, 1825. (Holotype: Brazil, Corcovado, *Raddi* FI not seen; isotype B)

P. elasticum L. C. Rich. ex Desv., Mém. Soc. Linn. Paris 6: 233, 1827, non *P. elasticum* Bory ex Willd., 1810. (Type: *P. elasticum* L. C. Richard, 1792, nom nud., was validated by Desvaux by accepting this name and citing *P. elegans* Poir. and *P. plumula* Humb. & Bonpl. ex Willd. as synonyms; the name is thus to be considered an illegitimate renaming. The name *P. elasticum* was subsequently accepted by Baker in Hooker & Baker, Syn. Fil., ed. 2, 332, 1874, who cited *P. plumula* as a synonym but not *P. elegans*, thus effectively fixing *P. plumula* as lectotype. Thus, *P. elasticum* is to be considered a superfluous renaming of *P. plumula* Humb. & Bonpl.)

P. pulchrum Mart. & Gal., Mém. Acad. Bruxelles **15**: 41, 1842. (Holotype: Mexico, Veracruz, Jalapa, ad quercos, 4000', *Galeotti* 6332 BR)

P. pectinatum var. *schkuhrii* (Raddi) Baker in Hooker & Baker, Syn. Fil., 333, 1867.

P. pulchrum Mart. & Gal. var. *minus* Fourn., Mex. Pl. **1**: 76, 1872 (nomen nudum).

Ctenopteris plumula (Humb. & Bonpl. ex Willd.) J. Smith, Hist. Fil., 185, 1875.

Rhizome short- to long-creeping, 5 (3-7) mm in diam; rhizome paleae narrow-triangular, red-brown, lustrous, basifixed, acuminate, non-comose or occasionally comose, non-clathrate, the margins regularly papillose; *fronds* 35 (20-60) cm long, approximate on the rhizome; rachis 4.5 (2-7.5) times as long as the stipe; stipe and rachis black, with scattered, long, acicular hairs, ctenoid hairs absent; rachis paleae broadly cordate with short-acuminate apex (in Central America), cordate- or hastate-acuminate (in Central America and the West Indies), or hastate and narrowly triangular (South America), basifixed or cordate, bullate or not, golden to red-brown, the margins toothed or papillate and occasionally fimbriate; *blades* narrow- to linear-elliptic, 28 (15-52) cm long, 4.7 (3-7.5) cm wide, cuneate or occasionally subtruncate at the base; segments 24 (16-40) mm long, 2.5 (2-3) mm wide, perpendicular to the rachis or slightly ascending, abruptly reduced to lobes at the blade base, linear, straight, obtuse, symmetrical and expanded at the base, herbaceous, entire, the spaces between the segments $\frac{1}{2}$ to 1 times the width of the segments; lamina with scattered acicular and clavate hairs; costa decurrent on the rachis, black, occasionally brownish near the rachis in Central America, with scattered, long, acicular hairs; costal paleae similar to those of the rachis but reduced; veins once (or twice)-forked, free; guard cells 34μ long; sori medial, round, with long, simple, clavate paraphyses; *sporangia* mostly with 3 or 4 two-celled capsular setae; spores reniform, slightly tuberculate, ca 50μ long; $n=74$.

Lectotype: Venezuela, Caracas, *Bredemeyer* Herb. Willd. no. 19655-1, photograph B, fragm. NY. Syntype: Venezuela, Caripe, Cumana, *Humboldt & Bonpland* 429 Herb. Willd. no. 19655-2, photograph B. The choice of lectotype is discussed below.

Habitat: epiphytic on tree trunks and branches, occasionally terrestrial or epipetric on wet swampy or montane forests, from sea level to 2600 m alt.

Distribution: Florida, West Indies, eastern Mexico, south to southern Brazil.—Fig. 9.

U. S. A.: FLORIDA: BREVARD CO: Indian River, *Whitney* 1875 (GH). CITRUS CO: Pineola *Noble* s.n. (FLAS); Pineola grottoes, *Evans* 2006 (MICH). DADE CO: Whiskey Creek, Everglades Ntl Pk, *Craighead* s.n., Jan 1960 (FLAS); SW of Royal Palm Pk, *Cuthbert & Small* s.n., 14 May 1919 (FLAS). HERNANDO CO: Brooksville, *Jones* 24 (US). HILLSBOROUGH CO: Hillsborough River St Pk, R21E, T27S, Sect 8, *Evans* 1186 (MICH); 10 mi NE of Tampa, *Correll* 5868 (GH, US). MARION CO: Ocala, *Smith* s.n., Apr 1879 (GH). MONROE CO: Aiken, Key Largo, *Pollard et al.* 203 (US). POLK CO: 12 mi E of Lake Marion, vic of Winter Haven, *McFarlin* 4112 (MICH). SEMINOLE CO: Oviedo, *Eaton* 1023 (GH); Sanford, *Rapp* s.n., Mar 1911 (FLAS). ST. JOHN'S CO: 14 mi W of St. Augustine, *Reynolds* s.n., in 1877 (US). SUMTER CO: Drake Point, Lake Astachula, *Smith* s.n., 29 Mar 1879 (US); Indian Field Ledges, *Evans* 1143 (MICH); Rutland Creek, *St. John* s.n., 22 Dec 1934 (FLAS); Wonders Hammock, *Smith* s.n., 21 Mar 1883 (GH, MICH, US). VOLUSIA CO: Enterprise, *Faxon* s.n., Apr 1873 (GH); Ormond Beach, *Freeman* 59323 (US).

MEXICO: TAMAULIPAS: NW of El Progreso, *Stanford et al.* 985 (GH, MO, US); Gómez Farías, *Palmer* 300 (GH, MICH, MO, US); S of Huisachal, *Stanford et al.* 2055 (US). SAN LUIS POTOSÍ: Los Caños, *Palmer* 263 (GH, MO, US); 4 mi W of Pendería, *Graber* 233 (US); Tamasopo Canyon, *Pennell* 17983 (US), *Pringle* 3392 (GH, MO); Tamaz-

unchale, *Lundell* 7104 (MICH), *Copeland* s.n., 27 Dec 1938 (MICH, US); E of Xilitla, *Mickel* 590 (TENN); NE of Xilitla, *King* 4354 (US); Xilitla Road 9 mi, *Kenoyer & Crum* 3993 (GH, MICH). VERACRUZ: E of Chavarillo, *Weatherwax* 181 (MO); Coatepec, *Sánchez* S. 245 (US); El Mirador, *Purpus* 16642 (US); Jalapa, *Johnson* s.n., Oct 1906 (US); Orizaba, *Seaton* s.n., 29 Aug 1891 (GH); Orizaba, Ojo de Agua, *Copeland* s.n., 4 Febr 1938 (MICH, US); Potrero Viejo, *Copeland* 126 (GH, MICH); Teocello Falls, *Rhoads* s.n., Mar 1899 (US). HIDALGO: Jacala, *Chase* 7426 (MICH, MO), 7458 (MICH), *Kenoyer*, 15 Nov 1937 (MO), *Lyonnet* 1299 (US); 41 mi N of Jacala, *Barkley* 17MO16 (MICH); Molango, *Moore* 1970 (GH). OAXACA: Santiago de Jocotepec, *Santos* 3378 (MICH, US). CHIAPAS: Munic. Pichucalco, *Gilly & Hernandez* X. 175 (MICH). CAMPECHE: Hacienda San Pablo, nr Champotón, *Collins* 50 (US).

GUATEMALA: EL PETÉN: San Clemente to Dos Arroyos, *Bartlett* 12820 (MICH, US); Tikal National Pk, *Lundell* 16748 (US); Uaxactum, *Bartlett* 12754 (MICH); Uaxactum to San Clemente, *Bartlett* 12810 (MICH). QUEZALTENANGO: Colahuaché, *Rojas* 549 (US); San Felipe, *Kellerman* 5575 (US). SUCHITÉPEQUEZ: Cuyotenango, *Rojas* 151 (US); Las Animas, *Shannon* 276 (US). RETALHULEU: San Felipe, *Kellerman* 5584 (US). SANTA ROSA: Ojo de Agua, *Heyde & Lux* 4083 (US).

BRITISH HONDURAS: COROZAL: Honey Camp, *Lundell* 537 (GH, MICH, MO, US), *Meyer* s.n., 22 July 1930 (US). BELIZE: Maskall, *Gentle* 1240 (US). EL CAYO: Cohune Ridge, *Lundell* 6460 (MICH); Mountain Pine Ridge, San Agustín, *Lundell* 6748 (MICH); Valentín, *Lundell* 6276 (MICH, US).

HONDURAS: COMAYAGUA: Agua Salada, *Williams & Molina* R. 11451 (GH); Siguatepeque, *Standley & Chacón* P. 6684 (GH). ATLÁNTIDA: La Fragua, vic of Tela, *Ames* 7 (US).

EL SALVADOR: AHUACHAPAN: Sierra de Apaneca, Finca Colima, *Standley* 20182 (US). SONSONATE: Izalco, *Standley* 22189 (US). SAN SALVADOR: *Calderón* 1274 (US). CUSCATLÁN: Colina de Santa Tecla, *Calderón* 1786 (US). SAN VICENTE: Volcán de San Vicente, *Standley* 21609 (GH, US).

COSTA RICA: ALAJUELA: Alajuela, *Scamman* 6122 (GH), *Alfaro* 6056 (US). SAN JOSÉ: Tablazo, La Uruca, *Beyer* 1 (US); *Hitchcock* s.n., 22-24 Oct 1911 (US); *Pittier* 1231 (US).

PANAMA: VERAGUAS: Bahía Honda, *Taylor* 1390 (MICH, US).

CUBA: ORIENTE: Finca Playucla, *Ekman* 4451 (US); Baracoa, *Shafer* 3927 (US); Gran Piedra, *Clément* 7156 (US); Loma Mensura, *Shafer* 3822 (US); Monte Verde, *Shafer* 8696 (US); El Cobre, *Pollard & Palmer* 394 (US); Loma del Gato, *Hioram & Clément* 6486 (US), León, *Clément & Roca* 9960 (US), *Clément* 400 (US).

DOMINICAN REPUBLIC: SANTIAGO: Vallecito, San José de las Matas, *Valeur* 465 (GH).

JAMAICA: Abbey Green, *Maxon* 10096 (GH, US), *Arntully*, *Orcutt* 3105 (MICH, MO); Chester Vale, *Philipson* 758 (US); Mt Horeb, *Taylor* s.n., 27 April 1956; Guys Hill P. O., *Proctor* 5119 (MO); nr Kingston, *Lehmann* 972 (US); Lucea, *Hitchcock* s.n., 5 Jan 1891; Marshalls Pen, *Proctor* 22898 (MICH); Silver Hill Gap, *Maxon & Killip* 1234 (GH, US).

PUERTO RICO: Las Mesas, nr Mayagüez, *Holm* 253 (GH, US).

GUADELOUPE: Camp Jacob, *Duss* 4093 (GH); St. Lelande (Grand-Val), *Questel* 1163 (US).

SURINAM: Avanavero Falls, *Stahel* 4600 (MO); Augustus Falls, *Tafelberg*, *Maguire* 24754 (US); Grassi Falls, Saramacca River headwaters, *Maguire* 24945 (GH, MO, US), 24005 (GH, MO, US).

BRITISH GUIANA: Kanuku Mts, Takutu River, *Smith* 3289 (GH, MO, US).

VENEZUELA: DELTA AMACURO: Lower Orinoco, Santa Catalina, *Rusby & Squires* 367 (US). MIRANDA: Guatopo Ntl Pk, *Steyermark* 90029 (US). CARABOBO: Maracai, *Vogl* s.n., (GH).

COLOMBIA: MAGDALENA: Santa Marta, Campo Alegre, *Smith* 1026 (GH); La Vuelta del Tigre, Minca Rd, *Bennett* 36 (US). SANTANDER: Río Suratá valley, betw E Jaboncillo & Suratá, *Killip & Smith* 16404 (GH, US). ANTIOQUIA: Frontino, West Andes of Antioquia, *Lehmann* 7408 (US). VALLE DEL CAUCO: Cauca Valley, E of Zarzal, *Pennell et al.* 8407 (GH, US). META: Los Llanos, Villavicencio, *Cuatrecasas* 4690 (US); nr Río Guatiquía, *Pennell* 1559 (US); Puerto López, *Little* 8358 (US); mouth of Río Atacuari, *Schultes & Black* 46-226 (GH).

PERU: SAN MARTÍN: Río Negro, *Woytkowski* 6198 (US); Tarapoto, *Woytkowski* 35134 (MO); Tingo María, *Allard* 20470 (US). LORETO: Maynas, Lupuna Cocha, *Tryon* 5186 (US); Mishuyacu, nr Iquitos, *Klug* 1382 (US); Santa Rosa, Urubamba Valley, *Cook &*

Gilbert 1727 (US). HUÁNUCO: Chinchao to Puerte Durend, *Coronado* 90 (GH, US); Yanayacu, *Bües* 2000 (US). JUNÍN: Colonia Perene, *Killip & Smith* 25047 (US), along Río Perene, nr "Hacienda 3," *Killip & Smith* 25169 (US); La Merced, *Killip & Smith* 23941 (US); Río Paucartambo Valley nr Perene Bridge, *Killip & Smith* 25382 (US); Schunke Hacienda, above San Ramón, *Schunke* A158 (US); nr San Ramón, *Coronado* 261 (GH); Manto, nr Yaupi, *Woytkowski* 6522 (US), 6393 (US), 6413 (US), 6479 (US); Yunguy, *Woytkowski* 6598 (US). cusco: Convención, *Herrera* 147 (US); Convención, Sahuayaco, *Vargas C.* 1825 (GH); Convención, Mission nr Quillabamba, *Mexía* 8090 (GH, MICH, MO, US), *Coronado* 112 (GH, US), *Soukup* 162 (GH); Potrero, *Tryon* 5390 (US); Playa Rosalina Río Alta Urubamba, *Bües* 1720 (US).

BOLIVIA: LA PAZ: Apolo, *Williams* 1120 (GH, MO, US); La Floride, South Yungas, *Buchtien* 483 (US); Mapiri, *Williams* 1118 (GH, US); Milluguaya, North Yungas, *Buchtien* 5004 (US); Polo-Polo, nr Coroico, North Yungas, *Buchtien* 3507 (GH, MO, US), 3507a (US); San Antonio de Mapiri, *Buchtien* 1074 (US); San Bartolomé (near Calisaya), South Yungas, *Krukoff* 10073a (MO); Tumupasa, *Williams* 1121 (US). SANTA CRUZ: Buena Vista, Prov Sara, *Steinbach* 5410 (GH); Espina, *Rusby* 136 (US); Motacucito, Sara, *Steinbach* 2506 (GH).

BRAZIL: AMAZONAS: Rosariulio, *Kuhlmann* 218 (MO). CEARÁ: Sitio Uruguaniana, 4 km W of Guaramiranga, *Cutler* 8318 (US). BAHIA: Monte Cruzeiro, *Rose* 20041 (GH, US); Rio Grongogy Basin, *Curran* 282 (GH, US); Toca de Onca, *Rose* 20076 (US). MINAS GERAIS: Ilhen, Fazenda da Tabunha, *Mexía* 4969-a (GH); Mariana, *Vanthier* 591 (GH). RIO DE JANEIRO: betw Alto da Serra & Meio da Serra, *Smith* 1553 (GH, US); Corcovado Mt, *MacGillivray* 149 (GH); Estrada Velha de Petropolis, *Smith* 6466 (US); Ilha Grande, *Rose* 20363 (US); Itaguaí, Rio Mazomba, *Brade* 20163e (MO); Organ Mts, *Wagner s.n.*, in 1901-1902 (MICH); Petrópolis, *Smith* 6466 (GH, MO); Rio de Janeiro, *Lindman* A159 (US), *Regnell* 250 (US), *Gaudichaud s.n.*, (GH).

This species has historically been broadly interpreted and frequently misconstrued. I have segregated out those entities which are clearly distinct, i.e. *P. bermudianum*, *P. dispersum*, *P. cupreolepis*, *P. ferrugineum* and *P. alfredii*, thus leaving a fairly uniform species but with some variation still to be more thoroughly explored. Figure 5 shows outline drawings of representative rachis paleae of specimens from different geographical areas. The broad cordate type from Central America appears to be the basic type and from that the narrower paleae of the West Indian plants and the extremely narrow paleae with large median marginal fimbriae of the South American plants have arisen as clinal modifications. The Central American plants with extremely cordate and golden rachis paleae also needs further study. These plants exhibit costae with brown bases and some brown streaking on the sides of the rachis. Although they are otherwise like the typical material, in these characters they show tendencies toward *P. alfredii* and *P. cupreolepis*. Their spores appear normal but no cytological information is known other than that *P. plumula* has been counted as a tetraploid in Florida and Jamaica.

A further question concerns a few collections from Brazil with only 32 spores in each sporangium. These spores are identical to the spores of the West Indian *P. dispersum*; and I have, therefore, included the specimens in that species. However, their morphology is closer to that of *P. plumula* than that of the typical West Indian *P. dispersum*. As I believe that *P. plumula* is probably one of the original parents of *P. dispersum*, it may be that the Brazilian *P. dispersum* is of different origin—possibly a hybrid between the southern *P. plumula* and *P. filicula*. There is, however, little evidence on which to base such an hypothesis and none of this material is known cytologically.

Polypodium elegans Poir. (1804), (non Cav. ex Swartz, 1806) has been referred to *P. plumula* (e.g. by C. Chr., 1906; de la Sota, 1960). However, the type (St. Dominique, Nectoux s.n., Herb. Webbianum, ex Herb. Desfontaines (FI) can be referred to *P. otites* L. (*P. tenuifolium* Humb. & Bonpl. ex Willd.). I have included *P. schkuhrrii* Raddi in synonymy. Though no type was designated, I have seen an illustration by Raddi (1825) and a Raddi collection (B) which fit his description (1819) and which I believe to represent an isotype. The type is probably at Firenze.

The choice of lectotype for *P. plumula* may be explained as follows. In the original description in 1810 of *P. plumula*, Willdenow attributed the name to Humboldt & Bonpland and cited the localities Cumana and Caracas, both in Venezuela. I have seen photos of the two syntypes in the Willdenow Herbarium in Berlin: Sheet 19655-2, collected in Cumana, Caripe, *Humboldt* 429, and Sheet 19655-1, collected in Caracas by Bredemeyer of which there is also a type fragment in NY. These two specimens represent different species in my opinion. In 1816, Humboldt, Bonpland, & Kunth described *P. plumula* again and a second species that they called *P. molle*, which are both represented in Paris by authentic specimens in the Humboldt & Bonpland Herbarium. The specimen called *P. plumula* and which agrees with their description corresponds with the Bredemeyer specimen in Berlin and the one called *P. molle* agrees with the *Humboldt* 429 collection in Berlin. Thus, Humboldt & Bonpland did collect two species both of which are represented in Paris but only one in Berlin. Since the original *P. plumula* was based on a mixture, one element has to be selected as lectotype. It should be considered that Humboldt, Bonpland, & Kunth did this in 1816 by keeping one element under the epithet *plumula* and describing the other as a different species, *P. molle*. Thus the *Humboldt* 429 specimen in Berlin was removed as *P. molle* from the concept of *P. plumula*, and inferentially the latter was left based on the Bredemeyer specimen, which is thus the lectotype. This specimen is conspecific with the Humboldt & Bonpland specimen in Paris which very likely originally provided the name. However, the Paris specimen can hardly be taken as lectotype since it may never have been seen by Willdenow at the time he drew up the original description. This Bredemeyer specimen represents a widespread species that has commonly been identified as *P. plumula*. The specimen *Humboldt* 429 at Berlin, the isotype of *P. molle* H.B.K. (which is a later homonym thrice over), represents a species that has also not usually been separated from *P. plumula* but which is different, as noted elsewhere, and which I am calling *P. dispersum*.

10. *Polypodium filicula* Kaulf., Enum. Fil., 275, 1824.

P. elasticum L. C. Rich. var. *filicula* (Kaulf.) Baker in Mart., Fl. Bras. 1(2): 517, 1870.

Rhizome short-creeping, 1-2 mm in diam; rhizome paleae narrow-ovate to narrow-triangular, brown, non-lustrous, basifixed, acute, non-comose, non-clathrate, finely serrate; *fronds* 10 (6-17) cm long, fasciculate on the rhizome; rachis 5.4 (3.5-11) times as long as the stipe; stipe and rachis red-brown, with scattered acicular hairs ca 0.3 mm long; rachis paleae numerous, conspicuous, cordate, bul-

late, acute, dark brown, finely serrate; *blades* narrow-ovate to narrow-obovate, 9 (5.5-15.5) cm long, 2.5 (1.5-3) cm wide, cuneate at the base; segments 15 (10-20) mm long, 1.5 (1-2) mm wide, perpendicular to the rachis or slightly ascending, not deflexed but reduced to lobes at the blade base, linear, herbaceous, obtuse or rounded, symmetrical and expanded at the base, entire or undulate, the spaces between the segments ca $\frac{1}{2}$ to 1 times the width of the segment; lamina glabrous or with scattered, short, clavate hairs; costa decurrent on the rachis, with scattered acicular hairs ca 0.25 mm long, without paleae; veins simple, free; guard cells ca 41μ long; sorus supra-medial, round, with short, simple, clavate paraphyses; *sporangia* without setae; spores globose-reniform, smooth, ca 50μ long.

Type: Brazil, *Chamisso s.n.* not seen, B(?) or LE(?).

Habitat: epiphytic, occasionally epipetric, in humid forests at 500-2200 m alt.

Distribution: western and central South America from Colombia to southern Brazil and northern Argentina.—Fig. 9.

COLOMBIA: NORTE DE SANTANDER: Culagá Valley, nr Tapatá, *Killip & Smith* 20162 (GH, US).

ECUADOR: CARCHI: km no 78, Río Blanco, Ibana to San Lorenzo, *Dodson & Thien* 1563 (US).

PERU: AMAZONAS: Bagua, Río Utcubamba, 40 km S of Bagua Grande, *Hutchison* 1472 (US). SAN MARTÍN: Tarapoto, *Woytkowski* 35236 (MO). CUSCO: *Bües* 1589 (US); Cusco to Santa Ana, *Herrera* 874 (US); Convención, Potrero, 8 km W of Quillabamba, *Tryon* 5373 (GH, US); Urubamba Machupicchu, *Vargas C.* 3346 (US); Urubamba Valley, *Herrera* 3297a (US); nr Urubamba River, *Heller* 2203 (US).

BOLIVIA: LA PAZ: Guanai to Tipuani, *Britton & Rusby* 1448 (MICH); Tigre Pata, *Williams* 1125 (GH, US). COCHABAMBA: Cañamina, *Rusby* 82 (US). SANTA CRUZ: El Fuerte, Jamaipata, *Steinbach* 8272 (GH); Tres Cruces, *Herzog* 1538 (GH, US).

BRAZIL: MINAS GERAIS: Serra da Mutuca, nr Vargem de Ouro Podre, *Williams & Vicente* 6196 (GH, US); São Sebastião do Paraíso, *Brade* 17968 (MO). GOIÁS: Jataí, Queixada, Rio Corrente, *Macedo* 21554 (MO, US). RIO DE JANEIRO: Estrada Velha de Petropolis, *Smith* 6468 (US); Rio de Janeiro & Bahia, *Webb s.n.*, in 1868 (US). PARANÁ: Jaguariaíva, *Dusén* 15925 (GH, MO, US). RIO GRANDE DO SUL: Pareci Novo, nr Monte Negro, *Beetle* 1753 (US); São Luís, Lato Pirabó, *Jurgens & Stier* (Rosenstock 256) (US).

PARAGUAY: Guarapi, *Balansa* 2874 (US); Cerros de Tobaty, *Hassler* 6172 (GH).

ARGENTINA: JUJUY: Ledesma, *Dinelli* 16726 (GH). MISIONES: Loreto, *Moreau s.n.*, 26 July 1931 (GH); San Ignacio, *Hunziker* 764 (MO), *Vattuone & Bianchi* 169 (US); Gobernador Roca, *Schwarz* 6297 (GH); San Ignacio, Cristóbal, *Ahumada & de la Sota* 51 (US); Yabebiry, *Moreau* 48162 (US).

Although I have not seen the type, there can be little doubt about the application of *filicula* to this very distinctive species. It is easily recognized by its small size, cuneate blade base, dark cordate rachis scales, unforked veins, and its geographical isolation from any other closely similar species except *P. plumula*. It probably arose initially from the stock of the latter species, but it is presently quite distinct from it in a number of characters.

This species, like *P. dispersum* and *P. plumula*, reproduces readily by root proliferations. Several herbarium sheets show this character well, and a few sheets show dense mats of juvenile plants similar to the dense populations of small sterile plants of *P. dispersum*. It is presumed that this habit is correlated with dryness and exposure of the roots through a thin substrate.

11. *Polypodium dispersum* A. M. Evans, Amer. Fern Jour. **58**: 173, pl. 27, 1968.

P. molle H.B.K., Nov. Gen. Sp. Pl. **1**: 8, 1816, non Schreb., 1771. (Type: Venezuela, Cumaná, Humboldt & Bonpland s.n. P not seen, fragment B)

P. pectinatum var. *squamosum* Lindm. Ark. Bot. **1**: 238, 1903. (Lectotype: Brazil, Mato Grosso, Fazenda Sao José, Regnell A2671 S. Syntypes: Jamaica, Herb. Alstroemer S-PA, and Herb. Casstroem S-PA; Bermuda, Herb. Farlow GH; Brazil, Rio de Janeiro, Mosen 113 B, S, S-PA)

P. microsorum Lindm., Ark. Bot. **1**: 239, 1903, p.p. as to Cuba, Wright 1051, not as to lectotype. (See *P. pectinatiforme*, which is *P. microsorum* Lindm., not Mett.)

Rhizome short-creeping, 5 (4-8) mm in diam; rhizome paleae narrow-triangular, red-brown, lustrous, basifixed, acuminate, slightly comose, non-clathrate, inconspicuously toothed; *fronds* 43 (27-63) cm long, approximate on the rhizome; rachis 3 (2.5-4) times as long as the stipe; stipe and rachis black, thinly pilose with acicular hairs, occasionally with ctenoid hairs; rachis paleae conspicuous, narrow-triangular, hastate, non-bullate, basifixed, dark red-brown with pale base, lustrous, acuminate, inconspicuously toothed, fimbriate at the base; *blades* narrow-triangular, 32 (17-48) cm long, 6.8 (4.5-9) cm wide, subtruncate to abruptly cuneate at the base; segments 35 (23-47) mm long, 4 (3-6) mm wide, perpendicular to the rachis, occasionally deflexed at the blade base, reduced (sometimes to mere lobes) at the blade base, herbaceous, obtuse, symmetrical at the base, entire, the spaces between the segments approximately equal to the width of the segments; lamina with few, long, acicular and clavate hairs; costa decurrent on the rachis, thinly pilose with acicular hairs, with reduced paleae similar to those of the rachis; veins twice-forked, free; guard cells ca 38 μ long; sori medial, round or occasionally oblong, with a few, simple, clavate, paraphyses; *sporangia* mostly with 2 (1-4) two-celled capsular setae; spores globose to ovoid, slightly tuberculate, ca 43 μ long, with irregular, incomplete or interrupted variable scar, 32 per sporangium; $n=111$ (apogamous); gametophyte strap-shaped, branched, with marginal rhizoids, often with stomates, but without sex organs, proliferating 1-3 apogamous sporophyte proliferations.

Holotype: Florida, Citrus Co, R20E, T21S, Sect 1, Pineola Grottoes, 21 Sept 1963, Evans 2008 MICH; isotypes TENN, US.

Habitat: epipetric (mainly limestone), occasionally terrestrial or epiphytic, on walls, in rocky hillsides, open woods, relatively dry areas, 100-2000 m alt.

Distribution: Florida, West Indies, eastern Mexico, through western South America to southern Brazil.—Fig. 9.

U. S. A.: FLORIDA: ALACHUA CO: Buzzard's Roost, Gainesville, Weber & West s.n., 18 Nov 1927 (FLAS), Knoppen s.n., 19 Mar 1928 (US); Devil's Mill Hopper, Gainesville, West s.n., 11 Apr 1926 (FLAS). BREVARD CO: Indian River, Palmer s.n., in 1899 (MO). CITRUS CO: Pineola, West & Arnold s.n., 13 Nov 1932 (FLAS); Lecanto, St. John 325 (FLAS). HERNANDO CO: Annutalaga Hammock, R19E, T21S, Sect 20 & 29, Evans 2012 (MICH); on left bank of Withlacoochee River, 13 mi NE from Brooksville, Smith s.n., 22 Mar 1883 (US); Brooksville, Garrett s.n., 10 Oct 1953 (FLAS); Istachatta, Underwood 287 (GH); nr Nobleton, Knoppen s.n., Mar 1928 (US). HILLSBOROUGH CO: Hillsborough River St Pk, R21E, T27S, Sect 8, Evans 1189 (MICH). MARION CO: Anthony, Sect 1, T14S, R21E, Ward 1871 (FLAS), Blake et al. s.n., 2 Apr 1950 (FLAS); Ocala, Smith s.n., Apr 1879 (GH), Shockley s.n., Mar 1878 (GH). MARTIN CO: Sewell's Point, Curtis 5861 (GH, FLAS, MO, US). MONROE CO: Key Largo, Small 7294 (US); Pumpkin Key, Small s.n., 9 Mar 1915 (FLAS), R40E, T59S, Sect 12, Evans 1165 (MICH). PASCO CO: Blandton,

Underwood s.n., (GH). SUMTER co: Drake's Point, Lake Astachula, *Smith s.n.*, 29 Mar 1879 (GH); Indian Field Ledges, R21E, T20S, Sect 34, *Evans 1142* (MICH).

MEXICO: TAMAULIPAS: Gómez Farias, *Palmer 562* (GH, US). SAN LUIS POTOSI: Tamasopo, *Pringle 3999* (GH, US). HIDALGO: km 350, coll. unknown, 28 Mar 1938 (MICH). VERACRUZ: Río Seco, nr Córdoba, *Woronow 3002* (US). OAXACA: Cerro Concordia, *Conzatti 3043* (US).

GUATEMALA: ALTA VERAPAZ: Chilaseo, *Salvin* (GH); Cobán, *von Tuerckheim s.n.*, July 1885 (GH, US).

BRITISH HONDURAS: EL CAYO: Camp Six-Vaca Road, *Lundell 6545* (GH), Mt Pine Ridge, Río On, *Lundell 6798* (MICH). TOLEDO: Toledo, *Peck 820* (GH).

HONDURAS: COMAYAGUA: Agua Salada, *Williams & Molina R. 11451* (US); Siguatepeque, *Yuncker et al 5729* (GH, MICH, MO, US). FRANCISCO MORAZÁN: Las Mesea, *Standley 28656a* (US), *Williams & Molina R. 10096* (US). COLÓN: Cuyamel, *Carleton 476* (US). EL PARAISO: 5 km from Yuscarán, *Molina R. 10053* (US).

CUBA: *Wright 1051* (B, BR, G, GH, MO, L, NY, S-PA, US). PINAR DEL RIO: Arroyo del Sumidero, *Shafer & León 13699* (US); Bahía Honda to El Rosario, *Shafer 12009* (US); El Guama, *Palmer & Riley 161* (US); Taco-Taco, *Baker 3803* (US). LAS VILLAS: Cienfuegos, *Combs 349* (GH, MO); Hanabanilla Falls, Trinidad Mts, *Britton et al. 4856* (US); Las Vegas de Mataquá, Buenos Aires, *Jack 6524* (MO); Mina Carlota, SE of Cumanayagua, Sierra de San Juan, *Howard 5656* (GH); Sierra Gavilán, above San Blas, *Morton 3992* (US), *4142* (US); Trinidad Mts, power plant at San Blas, *Howard 5388* (GH, MO). CAMAGUAY: La Gloria, *Shafer 102* (US). ORIENTE: El Cobre, *Pollard & Palmer 412* (US); Arroyo Jiménez, Pico Turquino, Sierra Maestra, *Ekman 14794* (US).

HAITI: Bayeus, *Loomis s.n.*, May 1927 (US); Diquini, *Miller s.n.*, Mar 1925 (US); Furcy, *Leonard 4757* (GH, US); Hinche, Massif des Cahos, M. Vaillecife, *Ekman 6121* (US), Hinche, Massif du Nord, M. Pinquois, *Ekman 6160* (US); Jean Rabel, *Leonard 13048* (US); La Vallee, Tortue I, *Leonard 11681* (GH, US), *11580* (US); Mission, Fonds Varettes, *Leonard 3646* (US); Petionville, *Leonard 4928* (GH, US), Petionville, Massif de la Selle, Momence River, *Ekman 1514* (US); Riviere Soleilhet, *Holdridge 2047* (MICH); St. Michel de l'Atalaye, Mt la Cidre, *Leonard 7610* (US), La Lomas, *Leonard 7499* (US).

DOMINICAN REPUBLIC: AZUA: Sierra de Ocoa, San José de Ocoa, Bejucal, *Ekman 11887* (US). BARAHONA: Aceitillar, Sierra de Batoruco, *Jiménez* (Marcano 3120) (US). LA VEGA: Cotuy, *Abbott 761* (US); Gajo de Constanza, *Jiménez 2111* (US). MONTE CRISTO: Arroyo Asiento Frío, Dist Monción, *Valeur 214* (MO). SANTIAGO: San José de las Matas, *Jiménez 926* (US), *861* (US). SANTO DOMINGO: Barrabas, *Raunkiaer 72* (US); San Pedro de Macorís, *Rose 4189* (US).

JAMAICA: *Herb. Alstroemer* (S-PA); *Herb. Casstroem* (S-PA). Castleton, *Maxon 824* (US), *758* (US); Flamstead, Port Royal Mts, *Maxon 8647* (US); Greenwood, 5 mi ESE of Little River P. O., *Proctor 3931* (US); Kingston, Long Mt, *Wilson & Webster 436* (US); Lydford P. O.; mine area, *Howard & Proctor 13501* (GH); Mandeville, *Maxon 2556* (US), *Orcutt 5021* (MO); Montego Bay, nr Salt Spring, *Maxon & Killip 1658* (GH); Río Bueno, *Proctor 16619* (MO); 1 mi S of Rudds Corner, *Proctor 22896* (MICH); Schwallenburgh, Mt Diablo, *Wilson & Webster 489* (US); Silver Hill Gap, *Maxon 1144* (US); St. Andrews, Mt James, *Maxon 8602* (US).

PUERTO RICO: 10 mi SW of Carolina, *Wagner s.n.*, in 1944 (US); Maricao, *Hess 243* (US).

VENEZUELA: MONARAS: betw Caripe & San Agustín, *Steyermark 61778* (US). DISTRITO FEDERAL: Caracas, *Bailey 464* (US); Chacaíto Gorge, *Pittier 9479* (US); betw Caracas & La Guaira, *Rose 21727* (US); betw Cotiza & Los Venados, *Allart s.n.*, Oct 1924 (US), *Vogl s.n.*, (GH).

COLOMBIA: MAGDALENA: Santa Marta, *Smith 1026* (MO, US). META: Puerto López, *Little 8290* (US). NORTE DE SANTANDER: Región del Sarare, La Cabuya, Cuatrecasas, *Schultes & Smith 12135* (GH, US).

ECUADOR: MANABAI: hills S of Olmedo, *Haught 3492* (GH, US).

GALÁPAGOS ISLANDS: ALBEMARLE ISLAND: Iguana Cove, *Snodgrass & Heller 133* (GH, US), *14* (GH). CHARLES ISLAND: *Stewart 967* (US), *968* (US). CHATHAM ISLAND: SW End, Middle region, *Baur 358* (GH); *Stewart 966* (US); NW Ansel region, *Schimpff 155* (GH, MO, US). INDEFATIGABLE ISLAND: Academy Bay, *Stewart 962* (GH, US), *Svenson 74* (US); SE side, *Stewart 964* (GH, US); Fortuna, *Howell 9278* (GH).

BOLIVIA: Porango, *Herzog 1496* (S). LA PAZ: Guanai to Tipuani, *Bang 1448* (GH, US). BRAZIL: CEARÁ: Sitio Urganiana, 4 km W of Guaramiranga, *Cutler 8318* (GH, MO). MINAS GERAIS: Ouro Preto, *Macedo 3074* (MO, US). MATE GROSSE: Buriti, nr Santa Anna da Chapada, *Malme (Regnell I 1716)* (S), *Regnell II 2482* (S). RIO DE JANEIRO: *Mosén 113* p.p (S-PA, not S).

This species was noted as distinct by Maxon, and numerous herbarium sheets at US from the West Indies and Florida are annotated with the epithet "*dispersum*" in his handwriting. Although Maxon never published it, I have adopted his epithet.

This species has a type of apogamous life cycle thus far unique among ferns, in which the spores number only 32 per sporangium and are formed by mitosis rather than meiosis (Evans, 1964). It reproduces commonly by root proliferations, often forming dense populations of sterile plants in this manner. A further discussion of the life cycle and reproduction of this species may be found above.

The similarity of this species to *P. atrum* is striking. They differ in that *P. dispersum* has broader rachis scales and the basal segments are only slightly or not at all deflexed. Of more fundamental importance, however, is that these two species reproduce very differently. *Polypodium atrum* has 64 spores per sporangium and therefore can be assumed to reproduce by the normal sexual process. *Polypodium dispersum* reproduces apogamously and has no sex organs on the gametophyte. This means that there is no possibility for interaction between these two species. *Polypodium dispersum* is a triploid and, on morphological grounds, I suspect it arose as a hybrid between *P. atrum* and *P. plumula*. *Polypodium plumula* is a tetraploid, so I predict that *P. atrum* is a diploid. As *P. atrum* occurs only in Mexico and northern Central America, *P. dispersum* perhaps arose there and then migrated to the other parts of its range.

The relationships between *P. dispersum* and *P. bermudianum* are discussed under the latter species. See also the discussion of *P. plumula* for comments on the typification of *P. molle* H.B.K.

12. *Polypodium atrum* A. M. Evans, sp. nov.—Fig. 18.

Rhizoma breviter repens, paleis lineari-triangularibus, basi affixis, castaneis, comosis, integris; frondes approximatae articulatae, ca 40 cm longae; stipites et rhachides rigidae nitentes nigrae, pilos dissitos aciculares gerentes; paleae rhachidis numerosae parvae anguste triangulares vel lineari-triangulares, castaneae integrae, basi saepe hastatae; lamina pectinata, anguste oblonga, ca 33 cm longa et 8 cm lata, basi subtruncata vel interdum abrupte cuneata; segmenta anguste ovata, ca 40 mm longa et 4 mm lata, apice obtusa, basalia paullo reducta et valde deflexa; lamina pilos dissitos aciculares ferens; venae liberae 2-furcatae; sporangia saepe cum 2-4 capsularibus paraphysibus; sporae globoso-reniformes, tuberculatae, ca 34 μ longae, 64 per sporangium. *P. disperso* simile, segmentis basalibus deflexis, paleis rhachidis angustioribus, et numero sporae differt.

Rhizome short-creeping, 4-6 mm in diam; rhizome paleae linear-triangular, expanded at the base, red-brown with lighter base, basifixed, lustrous, comose, entire; *fronds* 42 (30-65) cm long, approximate on the rhizome; rachis 3.5 (2.5-5) times as long as the stipe; stipe and rachis black, with scattered, long, simple,

acicular hairs; rachis paleae small, narrow- to linear-triangular, often hastate at the base, red-brown, entire; *blades* narrow-oblong, 33 (21-50) cm long, 8 (6-11.5) cm wide, herbaceous, subtruncate or occasionally abruptly cuneate at the base; segments 42 (32-60) mm long, 4 (3-7) mm wide, obtuse, symmetrical at the base in the upper half of the frond, with the lower edge perpendicular to the rachis in the lower half of the frond, entire, the basal segments slightly reduced and strongly deflexed, or occasionally abruptly reduced to auricles, the spaces between the segments equaling or exceeding the width of the segments; lamina with scattered acicular hairs and short, simple or occasionally forked clavate hairs; costa perpendicular to the rachis, black throughout or dark red-brown at the base, with scattered, long, acicular hairs; veins twice-forked, all free; guard cells ca 35μ long; sori medial, round, with long, simple, clavate paraphyses; *sporangia* mostly with 3 or 4 two-celled capsular setae $35-95\mu$ long; spores globose-reniform, tuberculate, ca 34μ long.

Holotype: British Honduras, El Cayo District, Mountain Pine Ridge, San Agustín, on boulders on bank of Río Frio, July-Aug 1936, *Lundell* 6639 US 1638286; isotypes GH, MICH.

Habitat: terrestrial or epipetric, woods, cliffs, river banks, 60-900 m alt.

Distribution: southeastern Mexico to British Honduras.—Fig. 9.

MEXICO: VERACRUZ: Atayac River, *Copeland* 16058 (MICH); Córdoba, La Luz, *Kerber* 97 (US); Córdoba, Metlac River, *Copeland* 124 (MICH, US); Córdoba, Mt Orizaba, *Seaton* 424 (GH, US); Córdoba, San Alejo Mts, *Couch* M26 (US); Córdoba, Monte de San Pablo, *Woronow* 2996 (US); Valle de Córdoba, *Bourgeau* 1432 (GH); Playa Azul, nr Catemaco, *Stoutamire* 3563 (TENN); Potrero Viejo, *Copeland* 123, 126 (MICH); San Andrés Tuxtla, Laguna Encantada, *Dressler & Jones* 77 (GH, MO, US); Zacualpán, *Purpus* 2165 (GH, MO, US). OAXACA: Tuxtepec, Chiltepec, *Martinez-Calderón* 693 (MICH, US); Mogoñe, *Orcutt* 5211 (MO). TABASCO: Balancán, San Isidro, *Matuda* 3372 (MICH, US). CHIAPAS: San Fernando de Tuxtla, *Collins & Doyle* 167 (US).

GUATEMALA: EL PETÉN: Chicbul, La Libertad, *Lundell* 3378 (US), 3378-A (MICH), La Libertad, *Lundell* 2980 (MICH), 4707 (US); Tikal Ntl Pk, Dos Aguadas, *Lundell* 15588 (US), Remate rd S of Tikal, *Lundell* 15878 (US). IZABEL: Cacao, betw Panzós & Senahú, *Barber* 197 (US).

BRITISH HONDURAS: EL CAYO: Camp Six-Vaca Rd, *Lundell* 6545 (MICH, US); Cohune Ridge, *Lundell* 6494 (MICH, US); San Antonio, *Bartlett* 13062 (MICH, US).

HONDURAS: SANTA BÁRBARA: San Pedro Sula, *Thieme* 5692 (GH, US). COMAYAGUA: Tiquitapa River, Los Dragos, Seguatépequi area, *Steeves & Ray* 435 (GH, US); Jutiapa, Seguatépequi area, *Steeves & Ray* 414 (GH). YORO: Aguan River valley, Coyoles, Los Flores, *Yuncker et al.* 8150 (MO, MICH); Río Pelo, Cordillera de Mico Quemada, *Ames* 25 (US). ATLÁNTIDA: La Ceiba, nr Cangrajal River, *Yuncker et al.* 8792 (MO, MICH, US).

The relationships of this species are discussed under *P. dispersum* and *P. bermudianum*.

13. *Polypodium absidatum* A. M. Evans, sp. nov.—Fig. 20.

Rhizoma longe repens, paleis anguste triangularibus, basi dilatatis, atro rubro-brunneis basi pallidoribus, acuminatis, comosis, integris vel inconspicue fimbriatis; frondes approximatae, stipitibus et rhachibus atro rubro-brunneis pilos aureis acicularibus praeditis; paleae rhachis inconspicuae filiformes integrae; laminae anguste ovatae, basi anguste cuneatae; segmentis ascendentibus acutis integris vel crenulatis, basi asymmetricis, infimis ad auriculas reductis; laminae subtus pilis dissitis acicularibus et pilis numerosis longis clavatis praeditae; costae valde decur-

rentes; venae unifurcatae; sori mediales, paraphysibus simplicibus clavatis praediti; sporangia plerumque setifera.

Rhizome long-creeping, 5 (3-7) mm in diam; rhizome paleae narrow-triangular, expanded at the base, dark red-brown, lighter at the base, lustrous, basifixed, acuminate, comose, non-clathrate, entire or inconspicuously fimbriate; *fronds* 38 (15-57) cm long, approximate on the rhizome; rachis 3.5 (2-5) times as long as the stipe; stipe and rachis dark red-brown, with golden, acicular hairs ca 0.5 mm long, ctenoid hairs present; rachis paleae inconspicuous, filiform, entire; *blades* narrow-ovate, 30 (12-46) cm long, 6.5 (3.5-9) cm wide, narrow-cuneate at the base; segments 33 (20-50) mm long, 3.5 (2-4.5) mm wide, ascending ca 20°-30° from the horizontal, reduced to auricles at the blade base, linear-triangular, coriaceous to herbaceous, acute, asymmetrical at the base, entire to crenulate; lamina with scattered acicular hairs ca 0.3 mm long, and with numerous, long, clavate hairs; costa strongly decurrent, with scattered acicular hairs ca 0.5 mm long; veins once-forked, free; guard cells ca 66 μ long; sori medial, round, with simple, clavate paraphyses ca 0.25 mm long; *sporangia* mostly with 2 capsular setae up to 0.25 mm long; spores reniform, tuberculate, ca 59 μ long.

Holotype: Colombia, Santander, Páramo de Romeral, *Killip & Smith 18518* US 1353919; isotype GH.

Habitat: montane forest, epiphytic, occasionally epipetric or terrestrial, 2800-4100 m alt.

Distribution: greater Antilles and western South America south to Bolivia.—Fig. 11.

CUBA: ORIENTE: Gran Piedra, *Clément 7155* (US).

DOMINICAN REPUBLIC: AZUA: top of La Pelona, *Ekman 13643* (US). LA VEGA: Sabana Alta, *Ekman 13794* (US).

JAMAICA: *Hart 45* (US), 771 (MO).

VENEZUELA: MÉRIDA: Laguna Negra, *Gines 1748* (US).

COLOMBIA: MAGDALENA: Páramos, Sierra Nevada de Santa Marta, *Seifriz 463* (US). SANTANDER: Páramo de Romeral, *Killip & Smith 18518* (GH, US); Páramo de Santurbán, Vetás, *Killip & Smith 17925* (GH). BOYACA: Valle de las Playas, *Grubb & Guymer P40* (US); Valle del Corallitos, *Grubb & Guymer P103* (US). VALLE: Páramo de Bavaya, Rio Bugalagrande, Corrales, *Cuatrecasas 20551* (US).

ECUADOR: CARCHI: Tufino, SE slopes of Volcán de Chile, *Wiggins 10605* (US). CUSCO: Quito, *Holdridge 1579* (US). PINCHINCHA: Mt Pichincha, *Holmgren 289* (GH, US), *Mille 15* (US), *Mille s.n.* (MO); *Sodirop s.n.*, in 1905 (US). NAPO-PASTAZA: Antisanilla, *Anthony & Tate 318, 319* (US); Mt Atazco, *Mille s.n.* (GH); Pifo, *Mille s.n.*, in 1899 (US).

PERU: LA LIBERTAD: Otuzco, Agallpampa, *López M. 1024* (US).

BOLIVIA: TARIJA: Padcaya, *Fiebrig 2875* (GH).

Although often identified as "*P. curvans*" or "*P. curvatum*" by various authors, the types of these taxa do not agree with this species. The affinities of *P. absidatum* are discussed below under *P. curvans* Mett.

14. *Polypodium curvans* Mett., Ann. Sci. Nat. (Paris) V, 2: 253, 1864.

P. curvatum sensu Mett., Abhandl. Senckenb. Naturf. Ges. Frankfurt 2(1): 58, 1856, non Swartz, 1801.

P. circinatum Sodirop, Crypt. Vasc. Quit. 333, 1893. (Type: Ecuador, Azuay, nr Cuenca, *Rimbach 35* Q?)

Rhizome short-creeping, 3 (2-5) mm in diam; rhizome paleae narrow-triangular, dark red-brown with a lighter base, lustrous, basifixed, acute to acuminate,

comose, non-clathrate, entire or inconspicuously fimbriate; *fronds* 43 (18-90) cm long, approximate to fasciculate on the rhizome; rachis 8 (3-14) times as long as the stipe; stipe and rachis dark red-brown, with scattered, golden acicular hairs up to 1 mm long, and with scattered, short, clavate hairs, ctenoid hairs inconspicuous or absent; rachis paleae inconspicuous, filiform, dark red-brown, entire; *blades* linear, 38 (15-80) cm long, 4.5 (2.5-10) cm wide, linear-cuneate at the base, often circinate at the apex at maturity; segments linear, 30 (13-53) mm long, 2 (1.5-3) mm wide, strongly ascending ca 45° above the horizontal, herbaceous, acute, asymmetrical at the base, confluent, widely-spaced and gradually reduced to mere auricles at the blade base, crenulate to crenate; lamina with numerous, long, clavate hairs up to 200 μ long, without acicular hairs; costa decurrent on the rachis, with scattered, acicular, golden hairs ca 0.75 mm long; veins once-forked, free; guard cells ca 43 μ long; sori medial, round, occupying most of the lamina, with simple, clavate paraphyses ca 200 μ long; *sporangia* with 1 or 2 capsular setae up to 200 μ long, the sporangial stalk with 2 columns of cells; spores reniform, tuberculate, ca 44 μ long.

Type: based on *P. curvatum* sensu Mett. Mettenius' description was based on a Lechler specimen from Peru. The locality and number are given in Mett. Fil. Lechl. 1: 7, 1856, as Agapata, Peru, *Lechler* 2006, which is thus the holotype (B?; isotype L, Morton photo 1859).

Habitat: in montane forests, epiphytic or epipetric, 1600-4000 m alt.

Distribution: Ecuador to western Bolivia.—Fig. 11.

ECUADOR: Quitensian Andes, *Couthouy s.n.* in 1855 (GH). PICHINCHA: Quito, *Jameson s.n.*, in 1848 (GH). CHIMBORAZO: W slope of E Cordillera of Ríobamba, *Rimbach* 27 (GH, US). NAPO-PASTAZA: Antisanilla, *Anthony & Tate* 322 (US); Cubillán, W slope, *Rimbach* 12 (US).

PERU: Agapata, *Hohenacker* 2006 (GH); Chasqui, *MacBride & Featherstone* 27 July-13 Aug, 1922 (US); Mayuyoc, *Bües* 1027 (US). JUNIN: Huancayo, *Killip & Smith* 22129 (GH, US), 23364 (US); Quebrado de Occopilla, *Soukup* 3642 (GH, US). APURIMAC: Prov Abancay, Ampay, *Stork et al.* 10626 (MO); Bosques de Ampay, *Vargas* 364 (GH, MO, US); Soccllaccasa Pass, Abancay-Cuzco trail, *West* 3820 (GH, MICH, MO). cusco: Camino al Ampay (Apurimac), *Santander & Vargas*, Aug 1937 (GH); Prov Convención, Santa Ana, Hacienda Potrero, *Herrera* 877 (US); Prov Paucartambo, Valle del Paucartambo, Hacienda Churu, *Herrera* 271 (GH, US), 1107, 1605, 1655 (US); Prov Urubamba, Chupani, *Vargas C.* 11130 (GH). PUNO: Carabaya, Ollachea to Puente Ackopampa, *Vargas C.* 3346 (MO).

BOLIVIA: LA PAZ: Pelechuco, *Williams* 2583 (GH, US).

Polypodium curvans is similar to *P. absidatum*, from which the former differs by having much smaller and more delicate fronds, strongly circinate at maturity, and longer hairs on the rachis and sporangia. The spore and guard cell sizes of *P. curvans* suggest that it may be a diploid, whereas the spores and guard cells of *P. absidatum* (see Table 3) are considerably larger and in the polyploid range. *Polypodium curvans*, *P. absidatum*, and *P. choquetangense* appear to be closely related species.

In superficial appearance, *P. curvans* strongly suggests ctenopteroid affinities. However, this is not confirmed in any of the critical criteria of sporangial stalks or spore shape, and it is probably placed in the *P. pectinatum* complex.

15. *Polypodium choquetangense* Rosenst., Meded. Rijks Herb. Leiden **19**: 18, 1913.

Rhizome long-creeping, 4-5 mm in diam; rhizome scales narrow-triangular, red-brown, lustrous, basifixed, acuminate, comose, non-clathrate, entire; *fronds* 55 (36-90) cm long, approximate on the rhizome; rachis 7 (3-10) times as long as the stipe; stipe and rachis dark red-brown, with very long, scattered, simple acicular hairs, and with long, irregular, ctenoid, clavate hairs, without paleae; *blades* narrow-ovate, cuneate at the base; segments linear, strongly ascending ca 25°-50° above the horizontal, reduced to auricles at the blade base, herbaceous, acute, with constricted attachments to the rachis, pinnatifid to a narrow wing along the costa; lamina essentially glabrous, with scattered clavate hairs; costa decurrent on the rachis, with scattered, long, acicular hairs; veins once-forked, free; guard cells ca 50 μ long; sori inframedial, round, with simple clavate paraphyses; *sporangia* without setae; spores reniform, tuberculate, ca 42 μ long.

Type: Bolivia, Hab. Choquetanga grande in silvis montanis ad arborum truncos, 3300 m alt, Oct 1911, *Herzog* 2387 L, S.

Habitat: wet rocks and tree trunks, montane forest, 2700-3500 m alt.

Distribution: known only from the province of Cochabamba, Bolivia (Fig. 11).

BOLIVIA: COCHABAMBA: Ayopaya, Sailapata, *Cárdenas* 3085a (US), 3167 (US); Choro, *Brooke* 6090 (G, S); Jatun Pino to Carrasco, *Cárdenas* 5939 (US).

This species is unique because of its deeply pinnate-pinnatifid blades. It is the only pinnate member of the *pectinatum* complex. The base of the frond matures and sheds spores while the apical portion is still juvenile and unfurling, showing an almost indeterminate growth unknown elsewhere in the group. The very sinuous, almost circinate rachis, the strongly ascending segments, and the very long hairs of the stipe and rachis are found only in this species and *P. curvans*, which is clearly its nearest relative.

16. *Polypodium bolivianum* Rosenst., Repert. Sp. Nov. **5**: 236, 1908.

P. carpinterae Rosenst., Repert. Sp. Nov. **22**: 16, 1925. (Holotype: Costa Rica, La Carpintera, 1850 m 10 Apr 1908, *Brade & Brade* 14, p.p., S-PA)

Rhizome long-creeping, 8 (6-10) mm in diam; rhizome paleae narrow- to linear-triangular, expanded at the base, dark red-brown with pale base, lustrous, basifixed, acuminate, comose, with hairs obscuring most of the paleae, densely and conspicuously fimbriate; *fronds* 75 (35-135) cm long, spaced ca 1 cm apart to approximate on the rhizome; rachis 3 (2-5) times as long as the stipe; stipe and rachis dark red-brown, with numerous, conspicuous, ctenoid hairs, occasionally with short, acicular hairs; rachis paleae inconspicuous, small, filiform, with fimbriate margins; *blades* narrowly triangular, 55 (28-107) cm long, 15 (10-27) cm wide, truncate or rarely the lower segments slightly shortened; segments 80 (45-145) mm long, 6 (4-9) mm wide, perpendicular to the rachis or the lower segments occasionally deflexed, coriaceous, obtuse to acute, entire, symmetrical at the base, often slightly constricted near the base; lamina with few, short clavate hairs ca 125 μ long; costae perpendicular to the rachis, with a few clavate and ctenoid hairs below, without paleae; veins 2 or 3 forked, free or occasionally partially anastomosing, obscure; guard cells ca 43 μ long; sori supramedial, round, with a few clavate

paraphyses ca 150μ long, and with a cluster of setiform hairs around the receptacle, these obscured in the mature sorus; *sporangia* without setae; spores reniform, tuberculate, ca 43μ long; $n = 37$.

Holotype: Bolivia, South Yungas, Sirupaya, nr Yanacachi, ca 16° lat, 2300 m, humid forests, 29 Nov 1906, *Buchtien* 481 S-PA; isotype US.

Habitat: in montane forests, epiphytic on tree bases and trunks, occasionally terrestrial or epipetric on mossy rocks, (200) 1000-2700 m alt.

Distribution: southern Mexico, through western South America to western Bolivia.—Fig. 8.

MEXICO: CHIAPAS: *Ghiesbreght* 394 (GH).

GUATEMALA: ALTA VERAPAZ: Finca Sepacuité, *Cook & Griggs* 462, 555 (US); Pansamalá, *von Tuerckheim* 644 (US).

HONDURAS: COMAYAGUA: Siguatepeque, *Standley* 56350 (US); El Achote, hills above Siguatepeque, *Yuncker et al.* 5973 (US); Barranco de Trincheras, nr Siguatepeque, *Morton* 7582 (US).

COSTA RICA: ALAJUELA: Palmira, Zarcero region, *Smith* 4332 (MO). HEREDIA: Vara Blanca, betw Poás & Barba volcanoes, *Maxon* 8329 (US). SAN JOSÉ: Río del Convento, valle de Díquis, *Pittier* 12112 (US); San Ramón, *Tonduz* 17604 (US), *Brenes* 14221 (US). CARTAGO: Pejivalle, *Standley & Valerio* 47053 (US); Santa Clara de Cartago, *Maxon* 8208 (US).

PANAMA: CHIRIQUI: Casita Alta, Volcán de Chiriquí, *Woodson et al.* 887 (MO, US); Cerro de la Horqueta, *Maxon* 5405, 5409, 5423 (US); Cerro de Lino, above El Boquete, *Maxon* 5216, 5216a (US); El Boquete, *Cornman* 839, 1276, 1327 (US), *Maxon* 5248, 5249 (US). DARIEN: Cana, *Williams* 847 (US).

VENEZUELA: ARAGUA: Colonia Tovar, *Pittier* 9358 (GH, US).

COLOMBIA: MAGDELENA: Santa Marta, Sierra de Onaco, *Smith* 1027 (GH, MO, US); Mt San Lorenzo, Santa Marta, *Seifriz* 36 (GH, US). SANTANDER: Cerro Armas, *Haught* 1958 (US); Las Vegas, *Killip & Smith* 21153 (US); Mt Peña Blanca, Charta, *Killip & Smith* 19284 (GH); Río Surata valley, above Surata, *Killip & Smith* 16569, 19284 (US). CUNDINAMARCA: Macizo de Bogotá, Quebrada Chica, *Schultes* 18579 (US), *Cuatrecasas* 5242 (US), *Black* 46-424 (GH); W of Salto de Tequendama, nr Ermitaño, *Uribe* 3352, 3354 (US). ANTIOQUIA: Boquerón, betw Medellín & Palmitas, *Hodge* 6600 (GH). CALDAS: Río Boquia, Salento, *Killip & Hazen* 8843 (GH, US); Río Santa Rita, Salento, *Killip & Hazen* 8995 (US). VALLE DEL CAUCA: Pavas, *Killip* 11660 (US); Río Cali, Pichindé, Alto de las Brisas, *Cuatrecasas* 18280 (US).

ECUADOR: IMBABURA: Río Chaluayaco, below Magnolia, lower Intag Valley, *Drew* E-604 (US). LEÓN: Hacienda Solento, nr Santa Rosa, Cantón, Pajii, *Mexía* 6684, 6684a (US). PICHINCHA: Mt Pichincha, *Mille* 16 (MO, US). GALÁPAGOS ISLANDS: Albemarle I, *Stewart* 963 (GH, US).

PERU: JUNÍN: Chanchosmayo valley, *Schunke* 118 (US); Huacapistana, *Killip & Smith* 24146 (US), *Coronado* 272 (GH); Oxapampa, *Soukup* 2347 (GH); E of Quimiri Bridge, nr La Merced, *Killip & Smith* 23958 (US); Vitoc, *Soukup* 4432 (US). CUSCO: San Miguel, Urubamba Valley, *Cook & Gilbert* 1752, 1762 (US).

BOLIVIA: *Bang* 2228 (US); *Bang s.n.* (MO). LA PAZ: Mapiri, *Rusby* 356 (US); Polo-Polo, Coroico, N Yungas, *Buchtien* 3510 (GH, US); Hacienda Simaco at Tipuani, *Buchtien* 5269 (GH, US); Yungas, *Rusby* 357 (US). SANTA CRUZ: Yungas de San Mateo, Comarapa, *Steinbach* 8430 (GH).

This very large fern with coriaceous, almost waxy, fronds, strongly truncate blade bases, and densely fimbriate rhizome scales is one of the most distinctive members of the *P. pectinatum* group. Its affinities are not clear, although the generally glabrous lamina and the obscure tuft of setose hairs around the sorus suggest a relationship to *P. ptilodon*. In northern South America the rhizome scales are less densely fimbriate, and it becomes more difficult to separate the species from

P. eurybasis, which generally has a more pubescent lamina, subtruncate blade with more acute and crenulate segments, and not so harsh a texture.

I have included here two collections from the Galápagos Islands that are subtruncate and have a few ctenoid hairs and a few long hairs on the brown rachis. These may represent an endemic species, but because the specimens are juvenile, I am tentatively placing them here where they fit most closely.

17. *Polypodium eurybasis* C. Chr., Svensk. Vet. Akad. Handl. III, 16(2): 71, t. 16, fig. 12, 13, 1937.

Rhizome long-creeping, 5-9 mm in diam; rhizome paleae narrow-triangular, light to dark red-brown, lustrous, basifixed, acute to acuminate, comose, non-clathrate, entire to inconspicuously fimbriate; *fronds* 28-130 cm long, approximate on the rhizome; rachis 3 (2-5) times as long as the stipe; stipe and rachis red-brown to dark red-brown, subglabrous to densely villose with acicular hairs, ctenoid hairs also present; rachis paleae inconspicuous, filiform or linear, entire; *blades* narrow-triangular to narrow-ovate, 20-88 cm long, 4-26 cm wide, subtruncate to abruptly cuneate at the base; segments 22-135 mm long, 3-9 mm wide, linear-triangular, narrow-triangular at the blade base, perpendicular to the rachis, straight or slightly falcate, herbaceous to subcoriaceous, acute, symmetrical at the base or with the lower edge approaching a right angle with the rachis, crenulate to crenate; lamina essentially glabrous, with simple and forked clavate hairs up to 200 μ long, and occasionally with scattered acicular hairs; costa perpendicular to, or slightly decurrent on, the rachis, with a few reduced ctenoid hairs and with scattered acicular hairs up to 0.5 mm long; veins once- or twice-forked, free; guard cells 44-50 μ long; sori medial, round, with simple or branched, clavate paraphyses; *sporangia* without setae; spores reniform, tuberculate, 40-44 μ long.

This is a widespread and variable species distinguished primarily by its subtruncate blades, sharply acute and crenate segments, prominent veins, and glabrous lamina. It is probably most closely related to *P. bolivianum*, from which some of the northern South American material is difficult to distinguish. It can be subdivided into three varieties.

1. Rachis densely villose; rhizome paleae entire.17c. *P. eurybasis* var. *villosum*
1. Rachis subglabrous to thinly pilose; rhizome paleae entire to inconspicuously fimbriate.
 2. Veins once (twice)-forked; segments straight, crenate or crenulate; rhizome paleae red-brown, inconspicuously fimbriate17b. *P. eurybasis* var. *glabrescens*
 2. Veins twice-forked, segments straight or drooping at the apex, crenulate; rhizome paleae dark red-brown, entire to inconspicuously fimbriate.17a. *P. eurybasis* var. *eurybasis*

17a. *Polypodium eurybasis* var. *eurybasis*.

Rhizome paleae dark red-brown, attenuate, *fronds* 74 (30-114) cm long; stipe and rachis dark red-brown, with scattered acicular hairs 0.5 to 0.75 mm long, and also with conspicuous ctenoid hairs; *blades* narrow-ovate, 55 (21-87) cm long, 11 (4.5-18) cm wide; segments 58 (22-95) mm long, 6 (3-8) mm wide, straight or slightly drooping near the apex, herbaceous, symmetrical and expanded at the base, crenulate; veins twice-forked; guard cells ca 50 μ long; spores ca 40 μ long.

Holotype: Haiti, Massif de la Selle, Marigot, Jardins Bois-Pin, ca 1900 m, 9 June 1928, *Ekman H10062 S*; isotypes B, US.

Habitat: terrestrial, epipetric or epiphytic on trunks or branches, in montane forests, 1000-2600 m alt.

Distribution: Cuba, Haiti, Venezuela.—Fig. 11.

CUBA: ORIENTE: Pico Turquino, *Ekman 5455* (US), Loma Regino, *Ekman 14605* (US).

HAITI: Massif de la Selle, Croix-des-Bouquets, *Ekman 3088* (US); Mission, Fonds Varettes, *Leonard 3990* (GH, US).

VENEZUELA: MONAGAS: Cerro de Turumiquire, *Tate 120* (US); Cerro Negro, above La Sabana de Las Piedras, NW of Caripe, *Steiermark 62080* (MO, US). DISTRITO FEDERAL: El Junquito, *Killip & Rohl 37168, 37190* (US). ARAGUA: Colonia Tovar, *Fendler 221B* (GH, MO). BOLIVAR: Ptari-tepuí, *Steiermark 59595* (US); Mt Roraima, *im Thurn 104* (US), *Steiermark 58741* (US).

See *P. eurybasis* var. *glabrescens* for discussion.

17b. *Polypodium eurybasis* var. **glabrescens** (Rosenst.) A. M. Evans, comb. nov.

P. lachniferum var. *glabrescens* Rosenst., Repert. Sp. Nov. 11: 57, 1912. (Holotype. Bolivia, N Yungas, Unduavi, 3400 m, *Buchtien 2770 S-PA*; isotype US)

P. lachniferum var. *glabrescens* f. *incurvatum* Rosenst., loc. cit. (as "*incurvata*"). (Holotype: Bolivia, N Yungas, Unduavi, 3400 m, *Buchtien 2769 S-PA*; isotype US)

Rhizome paleae usually not expanded at the base, light red-brown, basifixed, inconspicuously fimbriate; fronds 80 (28-120) cm long, rachis 2.5 (2-3.5) times as long as the stipe; stipe and rachis red-brown, thinly pilose to subglabrous with short acicular hairs, ctenoid hairs present; blades narrow-triangular to narrow-ovate, 56 (20-88) cm long, 12 (4-26) cm wide, subtruncate; segments 65 (22-135) mm long, 6 (3-9) mm wide; lamina essentially glabrous, with scattered, simple, clavate hairs ca 0.25 mm long; costae perpendicular to the rachis, with scattered acicular hairs up to 0.35 mm long; veins once (twice)-forked, prominent; guard cells ca 44 μ long; sori large, covering one-third to one-fourth of the width of the lamina, with simple, clavate paraphyses; spores ca 44 μ long.

Habitat: pendent epiphyte in wet, shady, montane forests, 1500-3600 m alt.

Distribution: Costa Rica to western Bolivia.—Fig. 11.

COSTA RICA: ALAJUELA: Zarcero, *Smith H 127* (MO). HEREDIA: Cerros de Zurquí, NE of San Isidro, *Standley & Valerio 50346* (US). SAN JOSÉ: Laguna de la Chonta, NE of Santa María de Dota, *Standley 42128* (US); Las Nubes, *Standley 38846* (US).

VENEZUELA: ARAGUA: Colonia Tovar, *Fendler 221* (US). MÉRIDA: La Venta, *Jahn 851* (GH, US). MONAGAS: Cerro de Turumiquire, *Tate 148* (US).

COLOMBIA: Mutis 3236, 3237 (US). SANTANDER: California, *Killip & Smith 16902* (GH, US); La Baja, *Killip & Smith 18135* (GH, US). CUNDINAMARCA: Bogotá, *Ariste-Joseph s.n.* (US); Guadalupe, Bogotá, *Haught 5040* (US); Macizo de Bogotá, Quebrada de las Delicias, *Cuatrecasas 5463, 5608, 5675* (US); Bogotá, Río San Francisco Valley, Montserrate, *Hawkes & García-Barriga 94* (US), *Ewan 16901* (US); Bogotá Plateau, San Cristóbal, *Niemeyer 175* (US); Bogotá, old San Cristóbal to Ubaque rd, *Schiefer 322* (GH); Sabana de Bogotá, *Pring 133* (MO); Mun Chipaque, *Gutierrez V. 50* (GH). CALDAS: Magana, Old Quindio Trail, *Killip & Hazen 9431* (US); Páramo de Buena Vista, *Pittier 1147* (US); Cabeceras del Río Palo, Quebrada de Santo Domingo, *Cuatrecasas 19265* (GH, US). NARIÑO: Córdoba, *Ewan 16235* (US); headwaters of Río Guapuscal, *Ewan 16553* (US); San José, below La Victoria, *Ewan 16218* (US); Soledad, *Ewan 16510* (US).

ECUADOR: PICHINCHA: Mt Pichincha, *Mille s.n.* (GH). NAPO-PASTAZA: Pifo, *Mille s.n.*, in 1898 (US).

BOLIVIA: LA PAZ: Unduavi, N Yungas, *Buchtien 2771, 2772* (US); Sirupayo, nr

Yanacachi, S Yungas, *Buchtien* 485 (US). COCHABAMBA: Prov Chapare, Incachaca-Chusi, *Steinbach* 9235 (GH, MO); Río Tocarani, *Herzog* 2275 (US); Prov Sacaba, *Steinbach* 5868 (MO).

Of the three varieties of *P. eurybasis*, this one appears to be the most generalized element. It is distinguished from var. *eurybasis* by a more glabrous lamina, lighter green foliage, paler and broader rhizome scales, usually more crenate segments, and usually only once-forked veins. It is closer to var. *villosum*, as discussed below.

17c. *Polypodium eurybasis* var. **villosum** A. M. Evans, var. nov.—Fig. 19.

P. eurybasi var. *glabrescente* simile, paleis rhizomatis semper integris et rhachidibus dense villosis differt.

Similar to var. *glabrescens* except rhizome scales with entire margins; stipe and rachis densely villose with acicular hairs ca 0.5 mm long; range of dimensions not so great; *fronds* 75 (40-130) cm long; *blades* 56 (30-84) cm long, 12 (8.5-21) cm wide; segments 62 (45-104) mm long, 5.5 (4-7) mm wide.

Holotype: Colombia, Cundinamarca, collected on rocky ridge in brush on foothills above Bogotá, just N of mouth of Quebrada El Obispo, 830 m alt, 10 Jan 1943, *Fosberg* 19688 US 2290492; isotype US.

Habitat: epiphyte, occasionally epipetric or terrestrial in rich humus, in montane forest, 220-330 (830) m alt.

Distribution: Panama to western Bolivia.—Fig. 11.

PANAMA: CHIRIQUÍ: Camp Aguacatal, *Maxon* 5300 (US).

VENEZUELA: DISTRITO FEDERAL: Avila de Caracas, *Vareschi* s.n., Feb 1963 (TENN).

COLOMBIA: *Mutis* 3235 (US); *Ariste-Joseph* s.n. (US). MAGDALENA: Santa Marta, *Carriker* 16 (US); Sierra de Perijá, Casacará Valley, 23 km E of Codazzi, *Grant* 10982 (US). CUNDINAMARCA: Boca de Monte, W margin, Sabana de Bogotá, *Cuatrecasas*, *Jaramillo* M. & *Huertas* 25809 (US); Bogotá, *Ariste-Joseph* 1919, 1920 (GH, US); Montserrate, above Bogotá, *Ewan* 16920 (US); Páramo de Cruz Verde, *Apollinaire* & *Arthur* 4 (US), *Cuatrecasas* 419 (US); Sibaté, *Pennell* 2494 (US). CALDAS: Pinares, above Salento, *Pennell* 9258a (US). CAUCA: Canaan, Mt Puracé, *Pennell* & *Killip* 6691 (GH, US).

ECUADOR: PICHINCHA: Corazón Peak & Corazón Pass, *Ewan* 16421 (US); Mt Pichincha, *Mille* 16 (US). CAÑAR: San Marcos, 5-8 km NE of Azogues, *Camp* E-2614 (US). AZUAY: N of Sevilla de Oro, *Camp* E-5209 (GH, MO, US). LOJA: Zamora-Huaico, *Espinosa* 2271 (US).

PERU: HUÁNUCO: Mito, *MacBride* & *Featherstone* 1621, 1731 (US); Muna, trail to Tambo de Vaca, *MacBride* 4280 (US).

BOLIVIA: LA PAZ: Soratá, *Williams* 2575 (GH, US). COCHABAMBA: Incachaca-San Antonio, Prov Chapare, *Steinbach* 8988 (GH, MO); Prov Sacabá, Cochabamba, *Steinbach* 5868 (GH, MO).

This variety is differentiated from var. *glabrescens* primarily on the basis of the more densely villose rachis and the entire rhizome scales. As they both cover essentially the same range, these apparently are not clinal variations, and appear sufficiently distinct to warrant formal recognition. The peculiar distribution and relationships of this variety to the other two suggest that, if this is truly a distinct variety, there may be an ecological isolation not evident from the data available.

18. *Polypodium pectinatum* L., Sp. Pl. 1085, 1753.—Fig. 20.

P. otites sensu Willd. in L., Sp. Pl. ed. 4, 5: 177, 1810, non L., 1753 (Based on *Vahl s.n.*, Herb. Willd. no. 19653, "Habitat in America," B-photo)

Goniophlebium pectinatum (L.) J. Smith, Lond. Jour. Bot. 4: 57, 1842.

P. pectinatum L. var. *majus* Kuhn ex Krug, Bot. Jahrb. Engler 24: 128, 1897, nomen nudum. (Based on: Santo Domingo, *Eggers 2595b*, c, d B; Dominica, *Eggers 12 B?*; Martinique, *Hahn 55 P*)

P. pectinatum L. var. *wagneri* sensu Jenm., Bull. Bot. Dept. Jamaica 4: 125, 1897. (Not as to basionym *Polypodium wagneri* Mett., a species of sect. *Goniophlebium*. Based on: Jamaica, *Jenman s.n.* NY)

Rhizome long-creeping, 6.5 (5.9) mm in diam; rhizome paleae linear-triangular, dark red-brown with pale base, basifixed, filiform at the apex, inconspicuously comose, non-clathrate, inconspicuously and sparsely fimbriate; *fronds* 60 (30-126) cm long, approximate on the rhizome; rachis 6 (3.5-9) times as long as the stipe; stipe and rachis light red-brown, thinly pilose with acicular hairs up to 0.5 mm long, usually much shorter, ctenoid hairs inconspicuous to very conspicuous; rachis paleae usually absent, when present inconspicuous, filiform and entire; *blades* linear-elliptic, 50 (24-113) cm long, 7.5 (4.5-10.5) cm wide, abruptly cuneate at the base; segments 37 (23-53) mm long, 4.5 (3-7) mm wide, perpendicular to the rachis, abruptly reduced to a few pairs of lobes at the blade base, straight or slightly falcate, obtuse, the base expanded on the rachis and symmetrical, herbaceous, entire; lamina puberulous with small fine acicular hairs up to 0.25 mm long, usually shorter, also with inconspicuous, clavate hairs up to 100 μ long; costa slightly decurrent on the rachis, the trichomes as on the lamina and with reduced ctenoid hairs; veins twice (once)-forked, partially to almost completely anastomosing except at the apex of the segments; guard cells ca 47 μ long; sori medial, round, small, with a few simple, clavate paraphyses; *sporangia* ca 180 μ in diam, usually with one inconspicuous clavate capsular seta ca 65 μ long; spores reniform, tuberculate, ca 45 μ long; $n=37$.

Type: There is no specimen labeled *P. pectinatum* in the Linnaean Herbarium, nor any specimen agreeing with the diagnosis; therefore, the species was evidently based only on the references cited. There were two of these: *Polypodium lonchitidis folio*, *Pet. fil.* 31. t.7.f. 14 and *Polypodium nigrum tenerius sectum*. *Plum. amer.* 26. t. 37 (The "*tenerius*" is an error of Linnaeus for "*tenuius*."). The Petiver figure is copied from Plumier, and therefore there is essentially only the Plumier citation left, automatically making the Plumier plate the lectotype. This question was put to Mr. J. E. Dandy of the British Museum (Natural History) and this is his conclusion also. The Plumier citation refers to his "Description des plantes de l'Amerique," 1693. The text indicates that his species came from "nos Antilles," i.e. from the French Antilles. In a later work, "Tractatus de filicibus Americanis," (p. 64, t. 83, 1705) Plumier repeated the same description and figure; he amplified the text by replacing "nos Antilles" by Martinique and by adding the locality Jamaica, on the basis of a publication by Sloane on Jamaica. Plumier's original description was thus based on one of his own collections from Martinique which is thus the type locality. In publishing *P. pectinatum*, Linnaeus picked up only the locality Jamaica in error. The only species of this group occurring in

Martinique is the species as I have delimited it here, which also does occur in Jamaica. Linnaeus' description of the rhizome as "nudo" was evidently taken from Plumier's illustration, in which the artist has omitted showing the rhizome scales, probably in order to show more clearly the leaf-scars (which are drawn in a very exaggerated way); no species of this alliance has or could be expected to have a naked (i.e. scaleless) rhizome.

Habitat: on limestone rocks or epiphytic on tree trunks and horizontal branches, occasionally terrestrial, in lowland or montane humid forest, from sea level to 1100 m alt.

Distribution: West Indies and Costa Rica to northwestern South America.—Fig. 10.

COSTA RICA: LIMÓN: Hamburg Finca, on the Río Reventazón, below Cairo, *Standley & Valerio* 48712 (MO, US). SAN JOSÉ: El General, *Skutch* 2153 (MO, US). CARTAGO: Tuis, *Tonduz* 11309 (US).

PANAMA: San Pablo, *Blake s.n.*, 8 July 1872 (GH). BOCAS DEL TORO: Chiriquí Lagoon, *von Wedel* 2611 (MO). COCLÉ: El Valle, *Allen* 228 (US); Penonomé, *Williams* 495 (US). CANAL ZONE: Frijoles, *Standley* 27571 (MO, US); Barro Colorado I, *Standley* 31410, 40973 (US); Río Indio de Gatún, *Maxon* 4855 (US); Río Medio, *Miller* 1729 (US).

CUBA: PINAR DEL RÍO: source of Río Taco-Taco, Sierra de Los Organos, *Morton* 4295, 4300, 4315, 4485 (US). ORIENTE: El Yunque, nr Baracoa, *Underwood & Earle* 1292 (US), *Pollard & Palmer* 183 (US); Las Ninfas, Guantánamo, *Hioram* 1458 (US); W of Santiago, *Graves* 1482 (US); 20 km SW of Compañía de Moa Mill, Sierra de Moa, *Howard* 5973 (MO); N spur of Sierra Maestra W of Río Yao, *Morton & Acuna* 3352 (US); Sierra Nipe, Loma Mensura, *Ekman* 3149 (US), *Woodfred & Shafer* 3119, 3210 (US), Río Piloto, *Ekman* 2100 (US); Yateras, Josephina, N of Jagüey, *Maxon* 4103 (GH, US); Yateras, S of Jagüey, *Maxon* 4219 (GH); Yateras, Monte Verde, *Maxon* 4325 (GH, US), *Shafer* 8701 (US), *Wright* 1017 (GH).

HAITI: Marmelade, *Leonard* 7289a (US); Pilbury Hill, *Miller* 188 (US).

DOMINICAN REPUBLIC: BARAHONA: *Fuertes* 1013 (GH); Paradis, *Abbott* 1580a (US). DUARTE: San Francisco de Macorís, La Bracito, *Abbott* 2033 (US). LA VEGA: Piedra Blanca, *Allard* 13814, 13990, 13974, 13988 (US). SAMANÁ: Laguna, *Abbott* 367, 369 (US); Rojo Cabo, *Abbott* 164, 1164 (US); Samaná, *Abbott* 490 (US); Sánchez, *Abbott* 112, 113 (US). SANTO DOMINGO: La Cumbra, *Raunkiaer s.n.*, 4 Aug 1906 (US); Mt Isabel de la Torre, *Eggers* 2595c, 2595d (B). SEIBO: Samaná Bay, *Miller* 1032 (US); 3-4 mi W of San Lorenzo Bay, *Abbott* 1273 (US).

JAMAICA: *Roper s.n.*, in 1895 (MO). Cinchona, *Clute s.n.*, 21 Febr 1900 (GH); Hartford, Priestman's River, *Maxon* 2525, 2538 (US); Hollymount, Mt Diablo, *Maxon* 2319 (US); John Crow Mts, E of Seamen's Valley, Portland, *Maxon & Killip* 239 (GH, US); Port Antonio, *Millspaugh*, 28 Jan-6 Feb 1899 (GH).

PUERTO RICO: Aibonito, *Hioram* 269 (US); betw Arecibo & Utado, *Britton & Cowell* 2048 (US); 8 mi SW of Carolina (US); El Yunque, *Scamman* 6560 (GH); *Wagner s.n.*, 16 Apr 1944 (US); El Yunque, Río Piedras, *Johnston* 750 (US); Loma Icaco, Sierra de Naguabo, *Shafer* 3393 (US); Mariaco, *Kuhn* 426 (US); Mayagüez, *Heller* 4492 (GH, MO, US); rd from Ponce to Adjuntas, *Underwood & Griggs* 765 (US); Adjuntas Rd, 7 mi from Ponce, *Heller s.n.*, 2 Dec 1902 (US); Sierra de Luquillo, *Dale s.n.*, Febr 1926 (MICH); Utuado, *Underwood & Griggs* 21 (US); Vega Alta, *Wagner s.n.*, 30 Jan 1944 (US).

LESSER ANTILLES: ST. KITTS: Nine Turn Gut, *Box* 267 (US); Phillips Level, *Proctor* 19556 (GH). MONTSERRAT: *Turner s.n.* (US); *Shafer* 748 (US); Centre Hills, Salem, *Proctor* 18837 (GH, US). GUADELOUPE: Camp Jacob, *Duss* 4094 (US); Bains Jaunes, *Questel* 3165 (US); Matouba, *Scamman* 8168 (GH). DOMINICA: Roseau Valley, *Hodge* 56 (GH); Morne Brule, Portsmouth, *Hodge* 57 (MO, US); Sylvania, *Hodge* 1151 (US); Morne Diablotin, *Hodge* 2703 (GH, US). MARTINIQUE: Fontaines Didier, *Duss* 1676 (GH, MO, US), *Hahn* 55 (P). ST. LUCIA: 2.5 mi SSE of Soufrière, *Proctor* 17869 (GH, US). ST. VINCENT: *Smith* 249 (GH). GRENADA: St George Parish, Grenville Vale, *Hunnewell* 19435 (GH), *Sherring* 42 (US); Grand Etang, *Beard* 1260 (MO, US); Mt Pleasant, *Milton*, 19 Mar 1924 (US). ST. EUSTATIUS: *Fairchild s.n.*, 22 Jan 1932 (US).

VENEZUELA: BOLÍVAR: Cerro Pijiguao, N end of Serranía Suapure, above Pijiguao, Wurdack & Monachino 41300 (US).

COLOMBIA: SANTANDER: Río Suratá valley, above Suratá, Killip & Smith 16569 (GH). META: Sierra de la Macarena, Caño, Entrada, Philipson & Idrobo 1755 (US). VAUPÉS: Río Guaviare, San José del Guaviare, Cuatrecasas 7468 (US). CHOCO: Negría, Río San Juan, Killip 35027 (GH, US), Primavera, Scolnik 1653 (US). CAUCA: Gorgona I, Taylor 1227 (US). NARIÑO: Río Oretopungo, nr Río Putumayo, above Puerto Asís, Ewan 16764 (US).

ECUADOR: MANABI: Salango, Haught 3372 (US); Quininde, Holdridge 1678 (US).

PERU: SAN MARTÍN: Tingo María, Allard 21442 (US); Boquerón Pass, Allard 21734 (US). LORETO: Pongo de Manseriche, Río Santiago, Mexía 6212 (GH, MICH, MO, US), 6368a (GH, US).

Polypodium pectinatum, as interpreted here on the basis of the type illustration mentioned above, agrees with the usual concept of the species as it occurs in the West Indies. This interpretation goes back at least to Swartz, who correctly understood the Plumier description and illustration. I have seen three specimens from the Swartz Herbarium in Stockholm which are labeled *pectinatum* by Swartz and which agree with my concept of the species. A number of specimens from the West Indies and elsewhere have been wrongly identified as *P. pectinatum*; these are now referred to *P. dispersum*, *P. ptilodon*, and other species.

This species is best characterized by the very short hairs of the lamina, the short sporangial setae, and the abrupt reduction in the segments to several pairs of mere lobes at the base of the blade. Morphologically, it is most similar to *P. camptophyllum* var. *camptophyllum*, which has much longer and more dense hairs and is a larger and coarser plant. Specimens of *P. pectinatum* from the Lesser Antilles tend to have somewhat longer, though sparse, hairs and have the basal segments more gradually reduced than is typical. However, these plants are clearly related to the other West Indian material of *P. pectinatum* and not to *P. camptophyllum* var. *camptophyllum*.

19. *Polypodium venturii* de la Sota, Opera Lilloana 5: 186, fig. 31, 1960.

Rhizome long-creeping, 5 (4-6) mm in diam; rhizome paleae narrow-triangular, dark red-brown, lustrous, basifixed, acute, conspicuously comose, subclathrate with lighter non-clathrate base, entire; *fronds* 55 (45-60) cm long, approximate on the rhizome; rachis 3 (2-5) times as long as the stipe; stipe and rachis red-brown, pilose with acicular, golden hairs, ctenoid hairs conspicuous; rachis paleae inconspicuous, filiform, entire; *blades* narrow-ovate, 40 (28-47) cm long, 8 (6.5-9) cm wide, cuneate to subtruncate at the base; segments 40 (33-45) mm long, 5 (4.5-5) mm wide, perpendicular to the rachis or slightly deflexed at the blade base, linear-triangular, straight, obtuse, subsymmetrical at the base, chartaceous-herbaceous, entire, spaces between the segments $\frac{3}{4}$ to 1 times the width of the segments; lamina thinly pilose with clear, acicular hairs ca 0.35 mm long and with scattered clavate hairs ca 150 μ long; costa decurrent on the rachis, the trichomes as on the lamina; veins once- or twice-forked, free or occasionally partially anastomosing; guard cells ca 56 μ long; sori inframedial to medial, round, with simple clavate paraphyses ca 0.2 mm long; *sporangia* without setae; spores reniform, tuberculate, ca 50 μ long.

Holotype: Argentina, Tucumán, Tafí, Yerba Buena, 800 m, 17 Apr 1921, *Venturi* 1232 LIL. Not seen, but de la Sota has verified my material.

Habitat: epiphytic or on fallen logs, in forests, 600-2700 m alt.

PERU: CAJAMARCA: Colasay, *Woytkowski* 7013 (US). LORETO: Pampayacu, *Kanehira* 183 (US).

ARGENTINA: TUCUMAN: Chichigasta, Las Pavas, *Venturi* 2974 (GH, US).

This species is similar to *P. camptophyllum*, from which it can be distinguished by the usually completely free venation, smaller sori, non-setose sporangia, and the softer, more delicate foliage.

Although the two collections from Peru are less pilose and the hairs longer, in other characters they agree well with the Argentinian plants.

20. *Polypodium pectinatiforme* Lindm., *Hedwigia* 43: 309, 1904.

P. microsorum Lindm., *Ark. Bot.* 1: 239, t. 11, fig. 2, 1903, non Mett., 1855. (Lectotype: Brazil, Rio Grande do Sul, Porto Alegre, *Regnell* I A381 S. Syntypes: Brazil, Rio de Janeiro, *Mosén* 114 S, S-PA; Minas Gerais, Caldas, *Mosén* 2195 C, M, S, S-PA; Rio Grande do Sul, Hamberger Berg & Colon, *Silveira Martins*, *Regnell* I A493 S, S-PA, US, 493½ S; Cuba, *Wright* 1051 B, BR, G, L, NY, S-PA).

P. pectinatum L. var. *truncatum* Rosenst., *Hedwigia* 43: 228, 1904. (Holotype: Brazil, Santa Catarina, Joinville, *Schmalz* 87 S-PA)

P. pectinatiforme Lindm. var. *hirsutum* Rosenst., *Hedwigia* 48: 139, 1906 (as "*hirsuta*"). (Holotype: Brazil, Rio Grande do Sul, Lagoa, *Stier* 255 S-PA)

Rhizome long- to short-creeping, 5 (2-10) mm in diam; rhizome paleae linear-triangular, dark red-brown with pale base, lustrous, basifixed, acute, inconspicuously comose, non-clathrate, entire; *fronds* 40 (12-65) cm long, approximate on the rhizome; rachis 7 (5-11) times as long as the stipe; stipe and rachis red-brown, thinly pilose with golden, acicular hairs up to 1 mm long, sometimes also villose with short acicular hairs, ctenoid hairs conspicuous; rachis paleae inconspicuous, filiform, entire; *blades* narrow-ovate, 35 (10-60) cm long, 9 (3.5-14) cm wide, cuneate at the base; segments linear to linear-triangular, straight, 40 (15-65) mm long, 3 (2-6) mm wide, perpendicular to the rachis, the basal segments strongly deflexed and shortened or reduced to auricles at the blade base, asymmetrical at the base, the lower edge perpendicular to the rachis, acute, herbaceous, entire to crenulate; lamina with numerous acicular hairs up to 0.3 mm long, also with occasional clavate hairs; costa perpendicular to the rachis, thinly pilose with long, acicular hairs up to 0.5 mm long, sometimes with ctenoid hairs; veins once (twice)-forked, free; guard cells ca 39 μ long; sori supramedial to sub-marginal, round, with very long, simple, clavate paraphyses overtopping the young sorus, these obscure in the mature sori; *sporangia* without setae; spores reniform, tuberculate, ca 47 μ long.

Type: based on *P. microsorum* Lindm., non Mett. The syntypes do not constitute a homogenous sample of the species, in that as presently construed *Wright* 1051 is *P. dispersum*, *Mosén* 2195 is *P. singeri*, and *Mosén* 114 in S is *P. ptilodon* var. *robustum*, but in S-PA is *P. pectinatiforme*.

Habitat: epiphytic, occasionally epipetric or terrestrial, in forests, 1400-1700 m alt.

Distribution: southern Brazil, northern Argentina and Paraguay.—Fig. 10.

BRAZIL: MINAS GERAIS: Caldas, *Regnell* 319 (MO, US); Serra de Caldas, *Mosén* 2198 (C, S, S-PA); Serra de Mutuca, beyond Barreiro, *Williams* 6642 (GH, US), 6644 (GH), Vargem de Ouro Podre, *Williams* 6196a, 6197 (GH). RIO DE JANEIRO: Rio de Janeiro, *Glaziou* 396 p.p. (BR, non P); *Mosén* 113 p.p. (S, non S-PA); *Mosén* 114 p.p. (S-PA, non S); Serra dos Orgãos, *Lüetzelburg* 6915 (MICH). SAO PAULO: Campos do Jordão, *Harshberger* 930 (US), *Leite* 388 (GH). SANTA CATARINA: Sombrio, *Reitz* C1159 (US); Lages, *Spannagel* (*Rosenstock* 396) (US), *Spannagel* s.n., in 1920 (US). RIO GRANDE DO SUL: Hamburger Berg, *Lindman* I.A. 493 (S, S-PA, US); São Leopoldo, *Rick* s.n. (GH); Silveira Martins, *Lindman* A. 493½ (S).

PARAGUAY: Caaguazú, *Hassler* 9084 (GH).

ARGENTINA: MISIONES: Yerbel Viejo, *Burkart* 1584 (GH).

Superficially, *P. pectinatiforme* and *P. paradiseae* are very similar. The latter is considerably larger, however, with segments more gradually reduced at the base of the blade, and with characteristically more strongly crenate and falcate segments with marginal sori. The rhizome scales of *P. pectinatiforme* are larger and only inconspicuously comose.

Rosenstock's *P. pectinatiforme* var. *hirsutum* applies to specimens with a more villose rachis. This may be a distinct taxon, but I do not have sufficient material at hand to evaluate it satisfactorily.

21. *Polypodium paradiseae* Langsd. & Fisch., Icon. Fil. 11, t. 11, 1810.

P. pectinatum L. var. *paradiseae* (Langsd. & Fisch.) Baker in Mart., Fl. Bras. 1(2): 517, 1870.

Rhizome long-creeping, 8 (6-10) mm in diam; rhizome paleae narrow-triangular, red-brown, lustrous, basifixed, acuminate, comose, non-clathrate, entire or with a few inconspicuous fimbriae; *fronds* 120 (70-170) cm long, spaced ca 2 cm apart on the rhizome; rachis 7 (4.5-11.5) times as long as the stipe; stipe and rachis red-brown, pilose with long, golden, acicular hairs, ctenoid hairs conspicuous; rachis paleae inconspicuous, filiform, entire; *blades* 100 (60-150) cm long, 16 (10-20) cm wide, narrow-rhombic, narrow-cuneate at the base; segments 80 (55-105) mm long, 6.5 (4-9) mm wide, linear-triangular, falcate, gradually shortened and deflexed to mere auricles at the blade base, coriaceous, acute, unequal at the base with the lower edge perpendicular to the rachis or incised, 24 (18-30) pairs of segments in the middle ¼ of the frond, crenate; lamina thinly pilose with golden, acicular hairs, ca 0.3 mm long and with scattered clavate hairs ca 0.25 mm long; costa perpendicular to or curved downward from the rachis, pilose with long, golden, acicular hairs ca 0.4 mm long; veins 2-3-forked, free; guard cells ca 43μ long; sori marginal to submarginal, round, with simple clavate paraphyses ca 0.25 mm long; *sporangia* without setae; spores reniform, tuberculate, ca 43μ long; $n = 37$.

Holotype: Brazil, Santa Catarina, Santa Catarina I, *Langsdorff* s.n. Herb. Fisch. LE; isotype Herb. Willd. B, photograph.

Habitat: terrestrial or occasionally epiphytic, in wet forests, up to 1600 m alt.

Distribution: southeastern Brazil.—Fig. 10.

RIO DE JANEIRO: Matto, Macieiras, Mt Itatiaia, *Smith* 1764 (US); Monte Serrat, Mt Itatiaia, *Smith* 2296 (GH); Serra do Itatiaio, *Dusén* 467 (US). SAO PAULO: Alto da Serra, *Wacket* (US); Campos do Jordão, *Bailey* 889 (US); Guarujá, *Dusén* 14213 (US). PARANÁ:

Alexandra, *Dusén* 17128 (GH); Serra do Mar, Desiro Ypiranga, *Dusén* 14471 (GH); Tacarachy, *Dusén* 6602 (GH, MO, US), 14743 (MO), 14743a (GH, MO). SANTA CATARINA: Santa Catarina I, Itacorobi, *Rohr* 1040 (US); Itajaí, Praia Braba, *Smith & Reitz* 6093 (US); Joinville, *Müller* (US); Mun. Pôrto União, Pinheiral by new airport E of Pôrto União, *Smith & Reitz* 8845 (US); Sombrio, *Reitz* 1750 (US). RIO GRANDE DO SUL: São Leopoldo, *Leite* 1462 (211), 1716, 1855 (GH), *Reitz* C679?; São Francisco do Paula, Vila Oliva, *Rambo* 31204 (MO); São Salvador, *Leite* 1934 (212) (GH).

This species appears to intergrade with *P. ptilodon* var. *robustum*. However, the marginal sori and the crenate, narrow segments, gradually reduced and deflexed at the base of the blade are characteristic of *P. paradiseae*. Also, if the total length of the blade is measured and then the numbers of pairs of segments counted in the middle fourth of the blade length, these two species are strikingly separated. In my test of this character *Polypodium paradiseae* had 24 (18-30) pairs of segments, whereas *P. ptilodon* (including all four varieties) had 16 (10-21) pairs. Applying a Mann Whitney-U test to samples of 10 fronds of each species, the two groups were found to be significantly different at the .002 level.

22. *Polypodium camptophyllum* Fée, Mém. Foug. 8: 86, 1857.

Rhizome short- to long-creeping, 5-10 mm in diam; rhizome paleae linear-triangular, dark red-brown, basifixed, filiform at the apex, comose, with linear non-clathrate cells, entire to slightly and inconspicuously fimbriate; *fronds* 1.6-16 dm long, closely spaced to approximate on the rhizome; rachis 1.5-7 times as long as the stipe; stipe and rachis light to dark red-brown, pilose with acicular hairs 0.4-1 mm long, ctenoid hairs present; rachis paleae inconspicuous, filiform, entire; *blades* narrow- to linear-ovate, 13-138 cm long, 4-17 cm wide, cuneate at the base; segments 20-90 mm long, 3-8 mm wide, perpendicular to the rachis, or slightly deflexed at the blade base, reduced to lobes or auricles at the blade base, slightly falcate to straight, herbaceous to coriaceous, obtuse to acute, the base expanded and symmetrical or the lower edge approaching a right angle with the rachis toward the base of the blade, or incised, entire; lamina pilose with pale acicular hairs up to 0.5 mm long, and with scattered, clavate, simple or forked hairs ca 0.2 mm long; costa decurrent on the rachis, with fine, pale, acicular hairs like those on the lamina or with coarser, longer and yellower hairs than those of the lamina; veins once- or twice-forked, free to completely anastomosing with a free included veinlet; guard cells 52-57 μ long; sori medial to supramedial, with long, simple or forked, clavate paraphyses; *sporangia* with 0-3 multicellular capsular setae up to 250 μ long; spores reniform, smoothish to tuberculate, 43-60 μ long.

Polypodium camptophyllum is a widespread and variable species, distinguished primarily by the long-pilose pubescence of the rachis and lamina. It is subdivided into four varieties showing varying degrees of similarity to *P. pectinatum*.

1. Fronds less than 30 cm long; veins once-forked, free throughout 22d. *P. camptophyllum* var. *abbreviatum*
1. Fronds greater than 30 cm long; veins twice-forked, partially anastomosing.
 2. Veins completely anastomosing except at the segment apex; receptacular paraphyses and laminar hairs forked with a clavate and a setose branch; rachis 2.5 (1.5-3) times as long as the stipe; basal segments only slightly reduced and perpendicular to the rachis; plants of Bolivia and southern Brazil 22b. *P. camptophyllum* var. *macedoi*

2. Veins only partially anastomosing; receptacular paraphyses and laminar hairs simple; rachis 4.5-(1.5-7) times as long as the stipe; basal segments reduced to auricles or strongly deflexed and only partially reduced; plants wide-ranging.
3. Rachis and costa pilose with soft hairs up to 0.5 mm long, the lamina the same; sori occupying half the width of the segment or less
22a. *P. camptophyllum* var. *camptophyllum*
3. Rachis and costa thinly pilose with scattered, harsh acicular hairs ca 0.75 mm long, the lamina thinly pilose with finer hairs ca 0.35 mm long; sori occupying most of the width of the segment
22c. *P. camptophyllum* var. *lachniferum*

22a. *Polypodium camptophyllum* var. *camptophyllum*.

P. cinerascens Lindm., Ark. Bot. 1: 238, t. 11, fig. 6, 1903. (Lectotype: Brazil, Rio de Janeiro, Regnell I 474 S, isoelectotypes BR, C, S, S-PA, US. Syntype: Regnell I A99 S, S-PA)

P. robustum var. *cinerascens* (Lindm.) Hassl., Trab. Inst. Bot. Farm. Buenos Aires 45: 69, 1928.

P. lachniferum Hieron., Bot. Jahrb. Engler 34: 515, 1904, p.p., not as to lectotype. (for typification, see below under var. *lachniferum*)

Fronde 70 (25-165) cm long, spaced ca 1 cm apart on the rhizome; rachis 4 (1.5-5.5) times as long as the stipe; stipe and rachis light red-brown, pilose with pale, acicular hairs up to 0.75 mm long; *blades* 58 (23-138) cm long, 9 (3.5-17) cm wide; segments 45 (15-90) mm long, 5 (4-8) mm wide, perpendicular to the rachis, reduced to mere lobes at the blade base, slightly falcate to straight, herbaceous; lamina pilose with pale, acicular hairs, all ca 0.5 mm long; costa with trichomes like those on the lamina; veins twice (once)-forked, usually partially anastomosing; guard cells ca 52 μ long; sori occupying half the width of the segment or less, with long simple clavate paraphyses; *sporangia* with 2 or 3 capsular setae ca 250 μ long; spores reniform, tuberculate, ca 54 (47-60) μ long, mostly with 64 normal appearing spores per sporangium; $n = 74$.

Holotype: Colombia, Norte de Santander, Environs of Ocaña, in 1850, Schlim 128, p.p. P; isotypes BR, G, K photograph, not L.

Habitat: terrestrial, occasionally epiphytic, in rocky soil or on rocks in forests, often in openings or at the edge of the forest, 350-2100 m alt.

Distribution: Costa Rica, Cuba, Jamaica, northwestern South America to southern Brazil.—Fig. 10.

COSTA RICA: LIMÓN: Guápiles, Standley 37291 (US).

PANAMA: PANAMA: 5 mi N of Cerro Azu, rd to Cerro Jefe, Blum et al. 1692 (FSU).

CUBA: ORIENTE: El Cristo, Ekman 1468 (US); Sierra Maestra, Termino del Cobre, Clément 1129 (US), Finca Reunion to Loma del Gato, Ekman 6925 (US); El Cobre, Pollard & Palmer 412 (GH, MO, US).

DOMINICAN REPUBLIC: BARAHONA: Montaña Nueva, SE of Polo, Howard 8431 (GH). SAN JUAN: Juan Santiago, Howard 9288 (GH, US); Hondo Valle, Howard 8753 (GH, US). SANTIAGO: Arroyo Juan Fino, Jicomé, Valeur 655 (GH, US). LA VEGA: Salto de Constanza, Jiménez 2215 (US); Salto de Jiménoa, Jarabacoa, Jiménez 1533 (US).

HAITI: Bombardopolis, Leonard 13457 (US); Dept l'Artibonite, Ennery, Leonard 9576 (US); Furcy, Leonard 4432 (GH, US); Massif du Nord, Hinche, Ekman 6166 (US); Marc Sal, Holdridge 1380 (US); Massif de la Selle, Petionville, Ekman 10024 (US); Mission, Fonds Varettes, Leonard 3958 (US); St. Louis du Nord, Leonard 14469 (GH, US); Dept du Nord, St. Michel de l'Atalaye, Leonard 7627 (GH, US).

JAMAICA: Abbey Green, Maxon 10060 (GH, US); above Cedar Valley, Silver Hill Gap, Maxon 10272 (GH, US); Cinchona, Clute s.n., 21 Febr 1900 (US); Cinchona to Morce's

Gap, Killip 204 (US); Port Royal Mts, Flamstead, Maxon 8683a (US); Mandeville, Gilbert s.n., Febr 1895 (MO), Maxon 2581 (US); Mocho, Catadupa, Maxon & Killip 1551 (GH, US); Moneague, St. Ann, Hunnewell 15217 (GH); Mt Diabolo, Maxon & Killip 469 (GH, US); St. Helen's Gap, St. Andrew, Maxon & Killip 631 (GH, US); Troy, Underwood 2930 (US), 3296 (US).

VENEZUELA: MONGAS: Quebrada Colorado Grande, SW of Caripe, Steyermark 61690a (US). DISTRITO FEDERAL: Quebrada de San Lázaro, nr Caracas, Pittier 9760 (US).

COLOMBIA: MAGDALENA: Haught 3942 (US); betw Pueblo Viejo & San Miguel, Seifriz 359x (US). BOLÍVAR: El Patico, Río Paez, Lehmann K. 110 (US). SANTANDER: Pica-Pica Valley, above Tapatá, N of Toledo, Killip & Smith 20191 (GH, US). VALLE: nr Corrales, Lehmann 4424 (B); El Naranjo, Río Dagua, Lehmann 5049 (B, US).

PERU: Cedrobamba, Herrera 1580 (US). HUÁNUCO: Chinchao to Puerte Durand, Coronado 91 (US). APURÍMAC: Quebrada Nataza, Vargas C. 2299 (US). CUSCO: Urubamba River, Machu Picchu, Heller 2206 (US), Herrera 3479 (US).

BOLIVIA: LA PAZ: Apolo, Williams 1124 (US); N Yungas, Milluhuaya, Buchtien 4235 (MO, US); Sirupaya, Yanucachi, S Yungas, Buchtien 482 (US); Tres Cruces, Herzog 1616 (US).

BRAZIL: MINAS GERAIS: Mun. Ouro Preto, Andorinhas, Macedo 2864 (MO); Mun. Ituiutaba, Aroeira, Macedo 2383 (MO); Mun. Nova Lima, Serra do Curral, Williams 6505 (GH); Regnell I A 99 (S).

This is the central and widespread variety which ties the four together. The other three were not, however, necessarily derived from this variety, though var. *macedoi* very likely has been. The var. *abbreviatum* has considerably smaller spores, suggesting that it is a diploid and may have arisen by divergence. The var. *lachniferum* can, in most cases, be distinguished by the rather coarse golden scattered hairs on the rachis and costa, the slightly to strongly deflexed lower segments often reduced and auriculate, and the sori, which occupy the major portion of the segment. However, the collections which I have range from the West Indies to Peru and show little variation between range limits and considerable intergradation throughout its range with var. *camptophyllum*. The range of this and related varieties is complicated by its extension over what I consider to be four geographical areas (see Figs. 8 & 10). At the overlapping of three of these distributional areas in northern South America, the representatives of the *P. pectinatum-plumula* complex in Colombia and Venezuela are often difficult to interpret.

The material of var. *camptophyllum* from the West Indies and from Colombia is somewhat different. In the West Indies the segments tend to be more obtuse and the plants somewhat smaller, the spores more irregular, and a few evidences of apogamy are suggested, as discussed below. The material from Colombia tends to be larger with straighter and more acute segments. The laminar trichomes are essentially identical throughout the range. In Brazil the plants again begin to exhibit segments which are more obtuse and falcate as in the West Indian material, except that the stipe is considerably longer, and the anastomosing of the venation is more complete, as in var. *macedoi*. Because few collections from this area have been examined and because there does appear to be sufficient difference between the long-stiped materials which I have called var. *camptophyllum* and var. *macedoi*, I am maintaining the latter as a distinct variety.

Throughout the range of this species the spores seem normal, though large and somewhat irregular. The spores are much like the large and somewhat irregu-

lar spores of *P. ptildon* var. *caespitosum*. A few of the specimens from Cuba and Jamaica have quite irregular reniform spores. They appear viable but are attached in pairs by the terminal ends; sometimes only by one end, thus making a double spore in a horseshoe shape; sometimes by both ends, making a deformed, doughnut-shaped, double spore. These may be apogamous hybrids. Further cytological and populational studies of *P. camptophyllum* are in progress, but it is suggested that these few plants may be isolated cases of apogamous reproduction. I have included these specimens with var. *camptophyllum* as they represent only a small fraction of the total material, and they cannot at present be distinguished other than by a critical observation of the spores.

22b. *Polypodium camptophyllum* var. **macedoi** (Brade) A. M. Evans, comb. nov.

P. macedoi Brade, Arq. Jard. Bot. Rio de Janeiro **11**: 30, t. 10, 11, fig. 3, 1951. (Holotype: Brazil, Estado de Minas Gerais, Ituiutaba, Macedo 1098 RB-63398 not seen, isotypes G, MO)

Similar to var. *camptophyllum*, except: rachis only 2.5 (1.5-3) times as long as the stipe; veins completely anastomosing or free at the apex only; lamina with forked, clavate-setose hairs; receptacular paraphyses consisting of forked hairs with one clavate and one setose branch; spores reniform, smoothish, ca 44 μ long.

Habitat: terrestrial in humid forests and along river banks.

Distribution (Fig. 10): BOLIVIA: LA PAZ: Polo-Polo, Corioco, N Yungas, Buchtien 3505 (US); Yungas, Rusby 357 (US).

BRAZIL: MINAS GERAIS: San Vicente, Mun. Ituiutaba, Macedo 1894 (S, US), 2302 (MO, US), 2383 (US), 2864 (US).

This variety is distinguished from var. *camptophyllum* on the basis of the completely anastomosing venation, longer stipes, and the presence of forked hairs on the lamina, as well as receptacular paraphyses consisting of one clavate and one setose branch.

Although in the original description Macedo considered this a goniophleboid *Polypodium* because of its venation, in all other respects this variety is typical of the *P. pectinatum-plumula* complex. The extent of the anastomosing of the venation is only an extreme expression of what occurs to a lesser extent in var. *camptophyllum* and in *P. pectinatum* s.s.

22c. *Polypodium camptophyllum* var. **lachniferum** (Hieron.) A. M. Evans, comb. nov.

P. lachniferum Hieron., Bot. Jahrb. Engler **34**: 515, 1904. (Lectotype: Ecuador, Mt Tunguragua, 1500-2500 m, Lehmann 458 B, isoelectotypes LE, US. Syntypes: Colombia, Cauca, Central Cordillera, nr Corrales, 2000-2800 m, Lehmann 4424 B; Colombia, El Valle, nr El Naranjó, on Río Dagua, 300-1000 m, Lehmann 5049 B, US) The Colombian collections are referable to var. *camptophyllum*.

Rhizome as in var. *camptophyllum* except the rhizome paleae with entire margins; fronds 46 (33-70) cm long, approximate on the rhizome; rachis 5 (1.7-7) times as long as the stipe; stipe and rachis light to dark red-brown, thinly pilose with coarse, golden, acicular hairs ca 1 mm long, ctenoid hairs conspicuous; rachis paleae inconspicuous, filiform, entire; blades narrow-ovate, 35 (25-60) cm long,

7.5 (5-11.5) cm wide, broad-cuneate at the base; segments 40 (25-60) mm long, 4.5 (3.5-5) mm wide, perpendicular to the rachis, slightly deflexed and reduced to auricles at the blade base, slightly falcate, herbaceous to coriaceous, acute, the lower edge perpendicular to the rachis or incised, entire; lamina thinly pilose with acicular hairs up to 0.35 mm long and with scattered clavate hairs; costa decurrent on the rachis, with scattered long hairs up to 0.75 mm long; veins twice-forked, free or occasionally partially anastomosing; guard cells ca 57μ long; sori medial, round, occupying most of the width of the lamina, with long, simple, clavate paraphyses; *sporangia* occasionally with one capsular seta ca 200μ long; spores reniform, smoothish, $54 (41-69)\mu$ long; $n=74$.

Habitat: epipetric or terrestrial, montane, on and about rocks on wooded mountain sides, 600-2300 m alt.

Distribution: Cuba, Jamaica, northwestern South America.—Fig. 10.

CUBA: ORIENTE: La Perla, *Shafer* 8474 (US); Loma del Gato, Cobre Range of Sierra Maestra, *León et al.* 10530 (US).

JAMAICA: Arntully, *Orcutt* 3105a (US); Blue Mt Peak, *Hitchcock* s.n., 13 Dec 1890 (MO); Chestervale, *Underwood* 1148 (US), Cinchona, *Maxon* 2596 (US), *Underwood* 473 (US), Cinchona Plantation, *Underwood* 1127 (US); Farm Hill, *Orcutt* 3402 (US); Port Royal Mts, Flamstead, *Maxon* 8683 (GH, US); Blue Mt range, Helen's Gap to Morce's Gap, *Chrysler* 1741 (US); Mandeville, *Churchill* s.n., 16 Mar 1897 (MO); Moody's Gap, *Maxon* 1207 (US); Cedar Valley, rd to Silver Hill Gap, *Maxon* 10306 (GH, US); *Churchill* s.n., 26 Mar 1897 (GH).

VENEZUELA: MÉRIDA: Mucurubá, *Gehriger* 195 (US); Páramo de la Sal, *Jahn* 632 (US).

COLOMBIA: MAGDALENA: betw Pueblo Viejo & San Miguel, *Seifriz* 378 (US), 384 (US). SANTANDER: California, *Killip & Smith* 18488 (GH, US); betw Piedecuesta & Las Vegas, *Killip & Smith* 15508 (GH, US). CUNDINAMARCA: Bogotá, Quebrada, *Ewan* 15593 (US); Suba Hill, Sabana of Bogotá, *Schiefer* 596 (US); Facatativa, *Ariste-Joseph* A190 (US); Pandi, *Perez* s.n. (Col 552) (US); mts W of Salto de Tequendama, *Uribe Uribe* 3382 (US). ANTIOQUIA: Bello, *Archer* 161 (US); Boquerón, *Daniel* 1634 (US); Copacabana, *Henri-Stanislas* 1606 (US).

ECUADOR: Grubi, *Mille* 14 (US). TUNGURAHUA: Baños, *Popenoe* s.n., 6 Mar 1921 (US). AZUAY: Cuenca, nr union of Ríos Tarqui & Yanuncay, *Prieto*, (Camp E-2658) (US); Río Milchichic, 5 km N of Cuenca, *Prieto* (Camp E-2735) (US). LOJA: San Lucas, *Dodson & Thien* 564 (US). NAPO-PASTAZA: betw Río Blanco & Río Verde, rd from Baños to Puyo, *Dodson & Thien* 1970 (US).

PERU: CAJAMARCA: Las Juntas, *Rose* 23221 (US). JUNÍN: Huacapistana, *Coronado* 275 (GH); Manto to Yaupi, *Woytkowski* 6518 (US), Manto, km 20, *Woytkowski* 6521 (US); Prov Tarma, 5 km SW of Huacapistana, 25 km NE of Tarma, *Tryon* 5426 (GH, US); nr Yaupi, *Woytkowski* 6414 (US). AYACUCHO: Ccarrapa, betw Huanta & Río Apurímac, *Killip & Smith* 22473 (US).

This variety is closely related to var. *camptophyllum*, the best differentiating characters being that var. *lachniferum* is generally a shorter plant, with distinctly deflexed, reduced and auriculate basal segments; and that there are two distinctly different sizes of acicular hairs on the frond. There are scattered but long and harsh hairs on the costa and rachis and shorter, finer hairs (not as dense as in var. *camptophyllum*) on the lamina. The sori cover almost the entire width of the segment, whereas in var. *camptophyllum*, the sori, in most cases, cover only a half or less of the width of the segment.

22d. *Polypodium camptophyllum* var. **abbreviatum** A. M. Evans, var. nov.—
Fig. 18.

A var. *camptophyllum* simile, frondibus ca 23 cm latis, approximatis, laminis ca 18 cm longis et 6 cm latis, basi late cuneatis, segmentis ca 30 mm longis et 3 mm latis, rhachide perpendicularibus basalibus paullo deflexis exceptis, venis 1-furcatis, liberis, soris medialibus, laminam subtus fere tegentibus, sporangii cum setis 2-capsularibus differt.

Rhizome as in var. *camptophyllum*; *fronds* 23 (15-30) cm long, approximate on the rhizome; rachis 4.5 (3.5-5) times as long as the stipe; stipe and rachis red-brown, pilose with clear, acicular hairs ca 0.4 mm long, ctenoid hairs present; rachis paleae inconspicuous, filiform, entire; *blades* narrow-ovate, 18 (13-25) cm long, 5.5 (4-7) cm wide, broadly cuneate at the base; segments 30 (20-40) mm long, 3 mm wide, perpendicular to the rachis except the lower few slightly deflexed, mostly expanded and symmetrical at the base except the lower few pairs of segments incised on the lower edge and gradually reduced to auricles, herbaceous, acute, entire, the laminar and costal trichomes as in var. *camptophyllum* except shorter; costa decurrent; veins once-forked, free; sori medial, round, covering most of the width of the frond; *sporangia* with two capsular setae ca 0.14 mm long; spores reniform, slightly tuberculate, ca 43 μ long.

Holotype: Peru, Cusco, Prov La Convención, Distr of Santa Ana, Hacienda Echarabi, 1300 m, Jan 1926, *Herrera* 872 US 1342112.

Habitat: terrestrial on rocky hillsides, 1300-1800 m alt.

Distribution (Fig. 10): PERU: CUSCO: 20 km N of Ollontaytombo, *Hitchcock* 22516 (US); Pampakjahu, *Coronado* 105 (US).

This is a local endemic. It is smaller than either var. *camptophyllum* or var. *lachniferum*. It is related to the former by the trichomes of the lamina and rachis and to the latter by the reduction and constriction of the basal segments. Except for the overall small size and the smaller, regular spores, it could easily be considered as a hybrid of the other two varieties.

23. *Polypodium ptilodon* Kunze, *Linnaea* 9: 42, 1834 (as "*ptiloton*," in error).

Rhizome long-creeping, 8 (5-12) mm in diam; rhizome paleae narrow-triangular, dark red-brown, lustrous, basifixed, acuminate, comose, non-clathrate, entire; *fronds* 27-170 cm long, closely-spaced to fasciculate on the rhizome; stipes 1-36 cm long; rachis 5-42 times as long as the stipe; stipe and rachis red-brown, with scattered acicular hairs up to 2 mm long, ctenoid hairs conspicuous; rachis paleae inconspicuous, filiform, entire to inconspicuously fimbriate; *blades* narrow-to linear-ovate, 25-130 cm long, 3.5-22 cm wide, narrow-cuneate at the base; segments 2-11 cm long, 3-10 mm wide, perpendicular to the rachis or slightly ascending, gradually reduced to lobes or auricles at the blade base, straight to sub-falcate, acute to rounded, expanded at the base and symmetrical or with the lower edge perpendicular to the rachis, herbaceous to coriaceous, entire (crenulate), the spaces between the segments $\frac{1}{2}$ to 1 times the width of the segments; 10-21 pairs of segments in the middle $\frac{1}{4}$ of the blade; lamina with scattered silvery

acicular hairs up to 0.35 mm long, more densely pilose in an oblong area around the sorus and with scattered clavate hairs; costa decurrent on, or perpendicular to, the rachis, with ctenoid hairs, and with scattered, golden, acicular hairs up to 2 mm long; veins 1-3(4)-forked, free; guard cells 44μ long; sori medial, round or occasionally oblong, with simple and branched, clavate paraphyses up to 165μ long; *sporangia* with 1-3 capsular setae $45-140\mu$ long; spores reniform, tuberculate, $41-52\mu$ long.

This species is subdivided into four closely related varieties. *Polypodium ptilodon* var. *ptilodon* is known to be a diploid, with small spores. The var. *caespitosum* is a tetraploid, with larger spores; var. *robustum*, with similar spores is presumed to be a tetraploid. The var. *pilosum* has medium-sized spores, and is a smaller plant than the other varieties, with longer hairs on the rachis and costae.

1. Stipe 2 (1-5) cm long; segments rounded to obtuse; hairs of the rachis and costa 1.5-2 mm long23d. *P. ptilodon* var. *pilosum*
1. Stipe 13 (3-36) cm long; segments obtuse to acute; hairs of the rachis and costa less than 0.75 mm long.
 2. Lower edge of the segments perpendicular to the rachis in the lower half of the blade; fronds 110 (50-170) cm long; spores ca 52μ long; Bolivia, Argentina, Paraguay, Uruguay, and southern Brazil ...23c. *P. ptilodon* var. *robustum*
 2. Upper and lower edges of the segments similar and equally expanded and adnate on the rachis; fronds 85 (30-115) cm long.
 3. Stipe 14 (12-17) cm long; fronds 95 (55-115) cm long; spores ca 41μ long; Peru and Bolivia23a. *P. ptilodon* var. *ptilodon*
 3. Stipe 9 (3-13) cm long; fronds 70 (30-105) cm long; spores ca 52μ long; Florida, West Indies, Mexico and Honduras.23.b. *P. ptilodon* var. *caespitosum*

23a. *Polypodium ptilodon* var. *ptilodon*.

Fronds 97 (55-115) cm long, spaced ca 1 cm apart on the rhizome; rachis 6 (4-7) times as long as the stipe; stipe and rachis pilose with golden acicular hairs ca 0.75 mm long; rachis paleae entire; *blades* narrow-ovate, 80 (45-100) cm long, 15 (10-18) cm wide; segments 70 (55-90) mm long, 9 (8-10) mm wide, gradually reduced to mere wings at the blade base, obtuse, expanded at the base and symmetrical, the spaces between segments approximately equal to the width of the segments, 14 (13-15) pairs of segments in the middle one-fourth of the blade; costa perpendicular to the rachis, with scattered acicular hairs up to 0.3 mm long; veins 2-or 3-forked, 41μ long; $n=37$.

Type: Peru, Dept San Martín, in woods at Pampayacu, July 1829, Poeppig s.n. Since the original in the Kunze Herbarium in Leipzig is presumed to have been destroyed, the duplicate at B is designated lectotype.

Habitat: dense forests, 1100-1700 m alt.

Distribution (Fig. 11): PERU: AMAZONAS: Río Utcubamba, Cerro Tapur, 40 km S of Bagua Grande, *Hutchison* 1470 (MICH). JUNIN: Chanchosmayo Valley, *Schunke* 126 (US); San Ramón, *Schunke* Hacienda, *Schunke* A151 (US).

BOLIVIA: LA PAZ: Polo-Polo, Corioco, N Yungas, *Buchtien* 3508 (MO, US), 3510 (US); Mapiri, *Rusby* 356 (US); Simaco, Tipuani Valley, *Buchtien* 5269 (GH).

This variety is a diploid with spores averaging ca 11μ shorter than either of the two other similar varieties. Inasmuch as var. *caespitosum* is known to be a tetraploid, one may presume that var. *robustum*, with the same spore size, is also

a tetraploid. It would appear that var. *ptilodon* was the original parental stock in the species. The var. *caespitosum* is so similar to var. *ptilodon* that it could be an autotetraploid, although its smaller size indicates that it could also be of hybrid origin with any of several other Caribbean species.

23b. *Polypodium ptilodon* var. *caespitosum* (Jenman) A. M. Evans, Amer. Fern Jour. **58**: 170, 1968.

P. pectinatum auct., non L., 1753.

P. pectinatum var. *caespitosum* Jenman, Bull. Bot. Dept. Jamaica **4**: 125, 1897. (Holotype: Jamaica, Old England, 4000 ft, *Jenman s.n.* NY, not K which is *P. consimile* var. *consimile*)

As in var. *ptilodon* except: *fronds* 70 (30-105) cm long; rachis 9 (6-14) times as long as the stipe; stipe and rachis red-brown to blackish; *blades* 60 (27-90) cm long, 12 (6.5-18) cm wide; segments 65 (35-85) mm long, 7 (4-10) wide, obtuse to acute; guard cells 50μ long; *sporangia* with 1 or 2 two-celled capsular setae ca 140μ long; spores ca 56μ long; $n=74$.

Type: Based on *P. pectinatum* var. *caespitosum* Jenman.

Habitat: terrestrial or on mossy tree bases or logs, occasionally epipetric, usually in damp woods, mountain slopes or ravines, from sea level to 1500 m alt.

Distribution: Florida, Greater Antilles, eastern Mexico to Honduras.—Fig. 11.

FLORIDA: BREVARD CO: N of Titusville, Turnbull Hammock, *Small & DeWinkler 10799* (US). CITRUS CO: Homosassa Springs, *Correll 5798* (MO); 3 mi NE of Lake Lindsey, *Cooley 5488* (FLAS, US); Pineola grottoes, *Evans 2005* (MICH). COLLIER CO: Fakahatchee, *Eaton 1133* (GH); Deep Lake, Royal Palm Hammock, *Scull s.n.* (FLAS). DADE CO: Hattie Bauer Hammock, *Small 7421* (US). HERNANDO CO: Annutalagga Hammock, NW of Brooksville, R19E, T21S, Sect 20 & 29, *Evans 2011* (MICH), *Garrett s.n.*, 18 Sept 1953 (FLAS); Brooksville, Choochahattie Hammock, *St. John et al. s.n.*, 13 Jan 1935 (FLAS); Istachatta, *Curtiss s.n.*, Aug 1897 (US); Pineola, *McFarlin 3618* (MICH); Brooksville, Spring Lake, *Perkins 65* (MO). HIGHLANDS CO: Avon Pk Wildlife Management Area, N end of Bill Bay, *Evans 1158* (MICH); Sebring, Highlands Hammock, *Correll & McFarlin 6247* (US); Parker I, 4 mi E of Childs, *Ward et al. 2420* (FLAS), *Correll 6174* (GH). HILLSBOROUGH CO: Hillsborough River St Pk, R21E, T27S, Sect 8, *Evans 2018* (MICH). LAKE CO: Eustis, *Nash s.n.*, 25-27 July 1895 (US); Seminole Springs, *West s.n.*, 15 Oct 1929 (FLAS). MANATEE CO: Manatee, *Garber 15* (FLAS, US). MARION CO: *Stevens s.n.*, May 1883 (MICH). ORANGE CO: Rock Spring, *Harper s.n.*, 11 Febr 1915 (US). PASCO CO: Blanton, *Small et al. 10858* (US). POLK CO: Fort Meade, *Smith s.n.*, Mar 1880 (US); 7 mi S of Lakeland, Scott Lake, *Sheridan s.n.*, 28 Nov 1958 (FLAS); Peace Creek, *Smith s.n.*, Apr 1880 (US); Winter Haven, Faulkner Hammock, *McFarlin 3547* (FLAS, MICH). PUTNAM CO: 4 mi W of Interlachen, *West & Arnold s.n.*, 29 May 1942 (FLAS). SEMINOLE CO: Sanford, Orange Co, *Rapp s.n.*, Mar 1910 (FLAS). SUMTER CO: Indian Field Ledges, R21E, T20S, Sect 34, *Evans 2004* (MICH, TENN); Camp's Grove, *St. John s.n.*, 4 Dec 1933 (FLAS). VOLUSIA CO: Halifax R, *Reynolds s.n.*, in 1877 (US); 5 mi SW of Port Orange, *Freeman 59327* (US).

MEXICO: TAMULIPAS: Gómez Farías, *Palmer 306* (US). SAN LUIS POTOSÍ: Hacienda de Tamasopo, *Pringle 3974* (GH, MO, US); 4.2 mi E of Xilitla, *Mickel 602* (MICH). VERACRUZ: Atoyac River, *Copeland s.n.*, 3 Mar 1938 (US); Córdoba, *Conzatti & González 575* (GH), *Fink 74a* (US), *Woronow 3093* (US); Zacualpán, *Purpus 15728* (MICH), *3818* (US).

HONDURAS: CORTÉS: Río Lindo, N of Lake Yojoa, *Morton 7665* (US).

CUBA: Loma San Juan, *Hioram 7064* (US). LAS VILLAS: Buenos Aires, *Howard 5246* (GH, MO), *Morton 4154* (US); Arroyo de Manaca, Herradura, *Britton 4997* (US). ORIENTE: La Perla, *León 3849* (US); Loma del Gato, *Clément 1172* (GH), *Hioram & Clément 6490* (US); Santa Ana, 6 mi N of Jaguey, Yateras, *Maxon 4212* (GH, US). PINAR DEL RIO: source of Río Taco-Taco, *Morton 4304* (US).

HARTI: Plaisance, *Leonard* 9383 (US); St. Louis du Nord, *Leonard* 14314 (US).

JAMAICA: Cinchona, *Clute* 321 (MO); Morce's Gap, *Hatch* 30 (US); Mount James, *Maxon* 8550 (US), 8608 (US); Silver Hill Gap, *Maxon* 1143 (US), *Maxon* 1145 (US); above Tweedside, *Maxon* 933 (US).

The affinities of the variety are discussed above under var. *ptilodon*.

23c. *Polypodium ptilodon* var. **robustum** (Fée) A. M. Evans, comb. nov.

P. robustum Fée, Crypt. Vasc. Braz. 1: 92, 1869. (Type: Brazil, Rio de Janeiro, Angra dos Reis, 16 June 1868, *Glaziou* 2407 BR, C, K photo, P, S, US)

P. robustum var. *cinerascens* f. *majus* Hassl., Trab. Inst. Bot. Farm. Buenos Aires 45: 70, 1928. (as "major"). (Holotype: Paraguay, Sierra de Amambay, *Hassler* 11327 G)

P. robustum var. *cinerascens* f. *minus* Hassl., loc. cit. (As "minor"). (Lectotype: Paraguay, *Hassler* 624 G. Syntype: Paraguay, nr Tobaty, *Hassler* 6281 G)

As in var. *ptilodon* except: *fronds* 110 (50-170) cm long; *blades* 90 (45-130) cm long, 14 (9-22) cm wide; segments 70 (40-110) mm long, 8 (5-11) mm wide, gradually reduced to auricles at the blade base, expanded and symmetrical at the base in the upper part of the blade, with the lower edge perpendicular to the rachis in the lower half of the blade, 16 (10-21) pairs of segments in the middle one-fourth of the blade; costa decurrent on the rachis, thinly pilose with golden, acicular hairs ca 0.5 mm long; spores ca 52 μ long.

Habitat: terrestrial, occasionally epiphytic or epipetric, in moist woods and along streams, up to 1400 m alt.

Distribution: Bolivia and eastern Brazil to northern Argentina.—Fig. 11.

BOLIVIA: LA PAZ: Tipuani, Hacienda Simaco, *Buchtien* 5249 (US).

BRAZIL: CEARA: Sitio Pe de Ladeira, 3 km E of Guaramiranga, *Cutler* 8324 (GH).

MINAS GERAIS: Fazenda de Aguada, Viçosa, *Mexia* 5180 (GH, MO, US). RIO DE JANEIRO: Meio de Serra, *Smith & Brade* 2290 (GH); Monte Serrat, Mt Itatiaya, *Smith* 2296 (GH); Nova-Friburgo, *Leite* 4816 (MO); Petrópolis, *Drogo* 324 (US); Rio de Janeiro, *Wilkes Exped.* in 1838-1842 (US); Tijuca, *Ball s.n.*, 22-23 July 1882 (GH); *Glaziou* 1725 (BR, C); *Mosén* 114 p.p (S, non S-PA). SAO PAULO: Igaúpe, *Brade* 7735 (US); Mun. Moji-Guacu, Fazenda Campininha, 6 km NNW of Padua Sales, *Eiten & de la Sota* 2123 (US), PARANA: Tibagy, *Reiss* 67 (GH). RIO GRANDE DO SUL: Mun. Rio Pardo, *Jürgens s.n.* (Rosenstock 422) (US); São Leopoldo, *Reitz* 168 (US).

URUGUAY: Montevideo, no data (MO).

PARAGUAY: betw Río Apa & Río Aquidaban, San Luis, *Fiebrig* 4417 (GH); Sierra de Maracajú, Igatimí, *Hassler* 5511 (GH); Villarica, *Jørgensen* 4605 (MO).

ARGENTINA: MISIONES: Iguazú, Puento Iguazú, *de la Sota & Cuezco* 1556 (US); Posadas, *Ekman s.n.*, in 1907-1908 (MO).

See under *P. paradiseae* and *P. ptilodon* var. *ptilodon* for comments regarding the affinities with var. *robustum*.

23d. *Polypodium ptilodon* var. **pilosum** A. M. Evans, var. nov.—Fig. 20.

A var. *ptilodonte* simile, frondibus approximatis vel fasciculatis, stipitibus brevibus pilis numerosis longis acicularibus (interdum pilis brevioribus) praeditis, rhachibus cum pilis eis stipitium similibus et paleis inconspicue fimbriatis praeditis, lamina lineari-elliptica, segmentis apice rotundatis, basi symmetricis, infimis numerosis reductis triangularibus, costis horizontalibus, pilis dissitis longis acicularibus praeditis, venis 1-vel 2-furcatis, sporangiis cum 2 vel 3 inconspicuis setis praeditis, sporis 47 μ longis differt.

As in var. *ptilodon* except: *rhizome* long-creeping to suberect; *fronds* 49 (27-73)

cm long, approximate to fasciculate on the rhizome; stipe 2 (1-5) cm long; stipe and rachis with numerous long acicular hairs 1.5-2 mm long, occasionally with shorter, acicular hairs; rachis paleae with inconspicuously fimbriate margins; *blades* linear-elliptic, 47 (26-70) cm long, 6.5 (3.5-9) cm wide; segments 32 (18-48) mm long, 5.5 (3-9) mm wide, reduced to numerous pairs of triangular lobes at the blade base, rounded at the apex, symmetrical at the base, the spaces between segments less than one-half the width of the segment; costa perpendicular to the rachis, with scattered long acicular hairs 1.5-2 mm long; veins once- or twice-forked; *sporangia* with 2 or 3 short, inconspicuous, capsular setae up to 45μ long; spores ca 47μ long.

Holotype: British Guiana, Demerara, Essequibo River, *Jenman s.n.* NY.

Habitat: epiphytic or occasionally epipetric in humid forests, 400-1000 m alt.

Distribution: TRINIDAD: Blanchisseuse Rd, *Homersley* 306 (US); Maracas, *Homersley* 30 (US), 88 (US), Morne Bleu, *Britton et al.* (US).

BRITISH GUIANA: Essequibo River, nr mouth of Onoro Creek, *Smith* 2781 (GH); Shodikar Creek (Essequibo tributary), *Smith* 3010 (GH).

VENEZUELA: NEUVA ESPARTA: Copey, *Gines* 3799 (US). MIRANDA: Guinand Estate (Cárdenas), Siquire Valley, *Pittier* 5949 (US). AMAZONAS: Cerro Duida, Cano Negro, *Steyermark* 57993 (US).

PERU: SAN MARTIN: Tingo Mariá, *Allard* 21541 (US). HUANUCO: Tingo Mariá, Río Huallaga, *Tryon* 5334 (GH, US). JUNIN: Santa Rosa, Pichis Trail, *Killip & Smith* 26201 (US).

BOLIVIA: LA PAZ: San Carlos, Mapiri region, *Buchtien* 208 (US), 1072 (US). COCHABAMBA: Antahuacana, *Buchtien* 2167 (US); Puerto Polonia, Río Coni, 14 km E of San Antonio, *Cárdenas & Cutler* 8324 (GH, MO).

BRAZIL: CEARA: Sitio Pe da Ladeira, 3 km E of Guaramirango, *Cutler* 8324 (GH, MO). RIO DE JANEIRO: Ilha Grande, *Rose* 20350 (US).

This is the most distinct of the varieties of *P. ptilodon* because of the rounded segments, the conspicuously longer hairs of the rachis and costa, and the very short stipe. It is like the other varieties in the curious distribution of acicular hairs only around the sorus (a character found only in this species) and in the gradual reduction of the basal segments. Superficially it resembles *P. consimile*, but the harsher texture, the trichomes of the lamina and costa, and the rhizome scales are different.

24. *Polypodium consimile* Mett., Ann. Sci. Nat. (Paris) V, 2: 253, 1864.

Rhizome short- to long-creeping, 5 (3-7) mm in diam; rhizome paleae linear-triangular to triangular, dark red-brown to blackish, lustrous, basifixed, attenuate to acute, non-clathrate to sub-clathrate, slightly comose to comose with hairs completely obscuring the paleae throughout the rhizome, entire; *fronds* 25-65 cm long, close-spaced to approximate on the rhizome; stipe short to almost lacking; rachis 6-20 times as long as the stipe; stipe and rachis light to dark red-brown, with few acicular hairs up to 0.75 mm long and with inconspicuous ctenoid and clavate hairs; rachis paleae inconspicuous, linear, entire; *blades* narrow-ovate, 23-60 cm long, 4-15 cm wide, narrow-cuneate at the base; segments 20-75 cm long, 5-11 mm wide, perpendicular to the rachis, reduced to numerous short lobes at the blade base, straight, herbaceous, obtuse to rounded, the base symmetrical, expanded and confluent throughout, entire, the spaces between segments narrower

than the segments; lamina essentially glabrous, with occasional long, acicular hairs and small scattered, clavate hairs; costa decurrent on the rachis, with trichomes like those of the lamina; veins twice-forked, free; guard cells ca 43μ long; sori inframedial, round, small, with simple and branched, clavate paraphyses up to 160μ long; *sporangia* golden or brownish, with or without capsular setae; spores reniform, tuberculate, ca 40μ long.

As here construed, this species consists of the two varieties discussed below.

1. Sporangia setose; rhizome paleae narrow-triangular, not obscured by dorsal hairs; blade 6.5 (4-11) cm wide.24a. *P. consimile* var. *consimile*
1. Sporangia without setae; rhizome paleae broad-triangular, completely obscured by dorsal hairs; blade 12 (10-15) cm wide.24b. *P. consimile* var. *pastazense*

24a. *Polypodium consimile* var. *consimile*.

P. consimile Mett. ex D. C. Eaton, Mem. Amer. Acad., n.s., **8**: 198, 1860, nomen nudum. (Based on: Venezuela, propre colonia Tovar, Fendler 220 B, GH, MO, US)

P. consimile Mett. var. *minus* Hieron., Bot. Jahrb. Engler **34**: 519, 1904 (as "minor"). (Lectotype: Colombia, Tolima, Río Ambica, 2000 m, Lehmann 2353 B fragment, isoelectotypes LE, US. Syntype: Venezuela, Aragua, Colonia Tovar, Moritz 255, p.p. These two collections were separated by Hieronymus as "Forma 1" and "Forma 2," without assigning formal names. The specimen of "Forma 1" is chosen lectotype)

P. pityrolepis Rosenst., Repert. Sp. Nov. **22**: 16, 1925. (Holotype: Costa Rica, Río Chris, Juan Vinas, 1200 m, 30 Mar 1910, Brade & Brade 694 S-PA; isotypes NY, US)

Rhizome paleae linear- to narrow-triangular, comose hairs not obscuring the paleae; fronds 40 (25-60) cm long; rachis 12 (6-17) times as long as the stipe; blades 36 (23-50) cm long, 6.5 (4-11) cm wide; segments 34 (20-55) mm long, 5 (4-9) mm wide; *sporangia* mostly with 2 capsular setae up to 80μ long.

Holotype: Colombia, Ocaña, Norte de Santander, 6000-7000 ft. Schlim 633 B; isotypes BR, G, L.

Habitat: mountain slopes, montane forest and ravines, terrestrial or on mossy tree bases, 300-2300 m alt.

Distribution: Hispaniola, Jamaica, Guatemala south to Colombia and Venezuela.—Fig. 8.

GUATEMALA: EL QUICHÉ: Chamá, Johnson 206 (US). ALTA VERAPAZ: Cubilquitz, von Tuerckheim s.n., Nov 1903 (US).

COSTA RICA: Cabeceras del Bkís, Pittier 10572 (US); Cooper 6057 (MO), Cooper s.n., Nov 1886 (GH). ALAJUELA: Zarcero, Smith 48/32, 48/137, 48/195, 48/242, 48/247 (US), F72 (MO). SAN JOSÉ: La Hondura, Standley 37801 (US); La Palma, rd to La Hondura, Scamman 7763 (GH); Las Nubes, Scamman 7229 (GH). CARTAGO: Cartago, Cooper s.n., Apr 1888 (GH, MO, US); Cerro de la Carpintera, Standley 34310, 35537 (US); Navarro, Rorres R. s.n., 20 Dec 1923 (US).

PANAMA: CHIRIQUI: Bajo Mona, mouth of Quebrada Chiquero, Woodson et al. 1028 (US); El Boquete, Cornman 893, 1177, 1198 (US); "Camp I," Holcombs Trail, 10 mi above El Boquete, Killip 5228, 5253 (US); above El Boquete, Río Panduro, Killip 5419 (US), Roballo Trail, Río Piarnasta toward the Cordillera, Killip 5424 (US).

DOMINICAN REPUBLIC: MONTE CRISTO: Las Rosas, Ekman s.n., 6 June 1926 (US).

HAITI: Furcy, Leonard 4611, 4728, 4776 (US); Massif de la Selle, Croix-des-Bouquets, Ekman s.n., 2 Apr 1925 (US); Mission, Fonds Varettes, Leonard 4022 (US).

JAMAICA: Clyde River, below Cinchona, Underwood 435 (US).

VENEZUELA: MONAGAS: Cerro de Turumiquire, Tate 103, 104 (US). DISTRITO FEDERAL: Cordillera del Avila, above Caracas, betw Los Venados & Papelón, Steyermark 55070 (GH, MO, US). ARAGUA: Colonia Tovar, Fendler 220 (B, GH, MO, US), 220B (GH, US).

COLOMBIA: SANTANDER: Río Suratá, above Suratá, Killip & Smith 16647 (GH, US). CUNDINAMARCA: Bogotá, Ariste-Joseph (GH, US).

Although superficially similar to *P. ptilodon* var. *pilosum*, this species differs in the shorter rachis hairs, the lack of the stiff hairs around the sori, and the segments with symmetrical bases.

There may be valid varieties in this species other than the var. *pastazense* discussed below. The plants from Central America, represented by *P. pityrolepis* Rosenst., tend to have a lighter brown, glabrous or subglabrous, narrower blade, shorter stipes, and darker brown sporangia than the material from elsewhere in the range. Venezuelan plants tend to have shorter, more clathrate, and less comose rhizome scales, almost golden sporangia, and darker brown rachises and longer stipes.

24b. *Polypodium consimile* var. **pastazense** (Hieron.) A. M. Evans, comb. nov.

P. pastazense Hieron., Hedwigia **48**: 257, t. 13, fig. 22, 1909. (Holotype: Ecuador, betw Baños & Jívaria de Píntuc in Pastaza Valley, *Stubel 1011 B*)

Rhizome paleae short, triangular, dark red-brown, acute, non-clathrate, comose with hairs completely obscuring the scales throughout the rhizome; *fronds* 54 (42-65) cm long, spaced ca 1 cm apart on the rhizome; rachis 15 (12-20) times as long as the stipe; stipe and rachis red-brown, glabrescent with short, acicular hairs; *blades* 50 (40-60) cm long, 12 (10-15) cm wide; segments 60 (45-75) mm long, 9 (6-11) mm wide, obtuse at the apex; *sporangia* without setae.

Habitat: epiphyte in montane forests, 325-2300 m alt.

Distribution: Colombia and Ecuador.—Fig. 8.

COLOMBIA: NARIÑO: betw Río Miraflores & Río San Martín, Volcán de Cumbal region, *Ewan 16157* (US).

ECUADOR: NAPO-PASTAZA: Andes, *Spruce 5260* (US); betw Puyo & Canelos, *Mexía 6832* (US); Hacienda La Mascota, Canton Mera, *Mexía 7016* (US). ZAMORA-CHINCHÉPE: Cordillera Cutucu, *Camp E-1393* (US).

In the original description, Hieronymus noted the similarity between his species and *P. consimile*. I believe that it is sufficiently distinct to maintain varietally, because of the more robust aspect, the more nearly glabrous lamina, non-setose sporangia, and particularly the complete obscuring of the rhizome scales by the dorsal hairs. The spore and guard cell sizes do not suggest hybridity or polyploidy, and it is probable that this is a local endemic variety just south of the broader range of var. *consimile* and undergoing allopatric speciation.

25. *Polypodium recurvatum* Kaulf., Enum. Fil. 106, 1824.

P. extensum Fée, Crypt. Vasc. Bras. **1**: 85, t. 28, fig. 3, 1869, non Forst., 1786. (Holotype: Brazil, Rio de Janeiro, *Glaziou 2403 B*)

P. paradisiastrum Fée, Crypt. Vasc. Bras. **1**: 90, t. 29, fig. 2, 1869. (Lectotype: Brazil, Rio de Janeiro, Corcovado, *Glaziou 974 P*, isoelectotype BR. Syntypes: Brazil, Rio de Janeiro, Corcovado, *Glaziou 396 P*, at BR is *P. pectinatiforme*, Brazil, Therezopolis, *Glaziou 1725 P*. *Glaziou 1725* at BR and C represent *P. ptilodon* var. *robustum*)

P. paraguayense Baker, Jour. Bot. **310**, 1878. (Type: Paraguay, forests nr base of Cerro Telado, nr Villa Rica, *Balansa 388 G*)

P. pectinatum L. var. *recurvatum* (Kaulf.) Sodiro, Crypt. Vasc. Quit. **335**, 1893.

P. paradisiastrum f. *crenulatum* Rosenst., Hedwigia **46**: 140, 1906 (as "crenulata"). (Holotype: Brazil, Santa Catarina, Lages, *Spannagel 145 S-PA*)

P. paradisiastrum forma *pectinatum* Rosenst., loc. cit. (as "pectinata"). (Holotype: Brazil, Rio Grande do Sul, Serra João, *Rodriguez, Jürgens 159 S-PA*)

P. recurvatum var. *minus* Rosenst. ex Hassl., Trab. Inst. Bot. Farm. Buenos Aires 45: 69, 1928. (Holotype: Paraguay, Hassler 3990 G; isotype B)

P. recurvatum var. *paraguayense* (Baker) Hassl., loc. cit.

P. recurvatum var. *subbipinnatifidum* Rosenst. ex Hassl., loc. cit. (Holotype: Paraguay, Hassler 12241b G)

Rhizome long-creeping, 6 (5-7) mm in diam; rhizome paleae narrow-triangular, light red-brown, non-lustrous, basifixed or basally cordate, acute, inconspicuously comose, non-clathrate, the margins inconspicuously papillate; *fronds* 53 (22-90) cm long, spaced ca 1 cm or less apart on the rhizome; rachis 2 (1.5-3.5) times as long as the stipe; stipe and rachis red-brown, with scattered, short acicular silvery hairs, ctenoid hairs absent; rachis paleae inconspicuous, filiform, entire; *blades* triangular to narrow-triangular, 36 (16-65) cm long, 14 (10-24) cm wide, truncate at the base; segments 72 (30-120) mm long, 4.5 (3-6) mm wide, perpendicular to the rachis, occasionally slightly ascending, sometimes slightly shortened at the blade base, straight or occasionally slightly falcate, often slightly constricted toward the rachis, herbaceous or coriaceous, acuminate, expanded and symmetrical at the base, entire (rarely crenate), the spaces between segments 1-3 times as wide as the segments; lamina glabrous; costa perpendicular to the rachis, with scattered, short, acicular hairs; veins twice-forked, free; guard cells ca 39μ long; sori medial, round, with simple, clavate paraphyses; *sporangia* with 2 (1-5) short capsular setae; spores reniform, tuberculate, ca 43μ long; $n = 37$.

Type: Brazil, Santa Catarina, Santa Catarina I, *Chamisso s.n.* B, LE.

Habitat: epiphytic, occasionally epipetric or terrestrial, in forest, 50-1000 m alt.

Distribution: southeastern Brazil and Paraguay.—Fig. 8.

BRAZIL: Campo da Lanca, *Annies s.n.* (Rosenstock 113b) (US). BAHÍA: Toca de Onca, *Rose 20101* (US). RIO DE JANEIRO: Itatiaia, *Rose 20591* (US); Meio da Serra, *Smith & Brade 2289* (GH); Nova-Friburgo, *Leite 4232* (MO); Organ Mts, *Rose 20792* (US), *Wilkes U. S. South Pacific Exp. no. 15* (GH); Sumaré, *Brade 20607e* (MO); Rio de Janeiro, *Monroe s.n.*, in 1864-70 (GH). SAO PAULO: Campos do Jordão, *Leite 3570* (GH), *Leite 3498* (MICH), *Porto 3089* (MO). PARANÁ: Desvio Ypiranga, *Dusén 8337* (GH, MO, US). SANTA CATARINA: Mun. Blumenau, *Smith & Reitz 6287* (US), Hausa, *Lüdenvaldt 1.860* (US); Horto Florestal I. N. P. Ibirama, *Reitz & Klein 3090* (US); Joinville, *Schmalz 87* (MO); Lages, *Spannagel 5, 69, 118* (US); Marata, Pôrto União, *Reitz 4709* (US); São Bento, *Dutsch s.n.* (Rosenstock 113a) (US); Sierra da Pedra, Ararangua, *Reitz C279* (US). RIO GRANDE DO SUL: São Salvador, *Leite 2639* (209) (GH).

PARAGUAY: Villarrica, *Jørgensen 4385, 4605* (MO), *Hassler 8781* (B, G); Colonia Presidente González, *Regnell I, A. 1813* (US).

This is a distinctive species because of its gray-green foliage, long-acuminate segments, strongly truncate blade, and bright, inconspicuously comose, rust-colored rhizome paleae. Its only really close relative is *P. hygrometricum*, which is smaller in all respects and has only once-forked veins and more obtuse segments.

Many of the specimens from Paraguay have a more herbaceous texture and wider and often deeply lobed segments. They are clearly *P. recurvatum*, although several specific, varietal, and formal names for these have been created. Even though the range of the Paraguayan materials might suggest it, these do not represent intermediates between *P. recurvatum* and *P. hygrometricum*, so far as I can determine.

26. *Polypodium hygrometricum* Splitg., Tijdschr. Nat. Gesch. 7: 409, 1840.

P. pectinatum L. var. *caliense* Hieron., Bot. Jahrb. Engler 34: 517, 1904. (Holotype: Colombia, El Valle, Cordillera Occidental de Cali, nr Las Juntas del Dagua, *Lehmann* 7668 B; isotypes LE, US)

P. truncatulum Rosenst., Repert. Sp. Nov. 9: 343, 1911. (Holotype: Bolivia, Antahuacana, valley of Río Espiritu Santo, *Buchtien* 2168 S-PA; isotype US)

Rhizome long-creeping, 4 (3-5) mm in diam; rhizome paleae narrow-triangular, sometimes expanded and cordate at the base, light red-brown, basifixed, acuminate, inconspicuously comose, non-clathrate, the margins inconspicuously papillate; *fronds* 27 (10-50) cm long, close-spaced to approximate on the rhizome; rachis 7 (3-15) times as long as the stipe; stipe and rachis red-brown to dark red-brown, pilose with short to long, simple, acicular, silvery hairs, ctenoid hairs absent; rachis paleae inconspicuous, filiform, entire; *blades* 23 (8-40) cm long, 5 (2-9) cm wide, narrow-ovate to narrow-triangular, subtruncate to truncate at the base; segments 25 (10-45) mm long, 4 (2-5) mm wide, perpendicular to the rachis or slightly ascending throughout, narrow-ovate to linear-triangular, herbaceous, obtuse to acute at the apex, expanded and symmetrical at the base, entire; lamina pilose with simple, silvery, acicular hairs, clavate hairs absent; costa decurrent on the rachis, brown or occasionally stramineous or blackish, pilose as on the lamina; veins once-forked, free; guard cells ca 43 μ long; sori medial, round, with short, simple, clavate paraphyses; *sporangia* with 2 (1-5) acicular capsular setae; spores reniform, tuberculate, ca 48 μ long; $n = 37$.

Holotype: Surinam, Para, *Splitgerber* 1069 L.

Habitat: epiphytic, occasionally epipetric or terrestrial, in humid forests, 30-1800 m alt.

Distribution: southern Mexico to western Bolivia.—Fig. 8.

MEXICO: CHIAPAS: Escuintla, Col. Cintalapa, *Matuda* 18392 (US), Esperanza, *Matuda* 18116 (US); Huixtla, *Purpus* 7226 (GH, US).

GUATEMALA: RETALHULEU: Río Xibana, Finca San José Nil, *Hatch & Wilson* 403 (US); Pueblo Nuevo, *Rojas* 548 (US).

HONDURAS: COLÓN: Claura, *Spinden* 38 (US).

NICARAGUA: MANAGUA: Sierras de Managua, *Chaves* 7 (US).

COSTA RICA: Río Poás, *Pittier* 2426 (US). LIMÓN: La Columbiana Farm, *Standley* 36896 (GH, US). HEREDIA: La Selva, Río Puerto Viejo, *Scamman & Holdridge* 8098 (GH), *Scamman* 7518 (GH). SAN JOSÉ: El General, *Skutch* 2667 (MICH, MO, US); San Isidro del General, *Chrysler & Roever* 5318 (MICH, US). CARTAGO: Jesús María, *Lankester* 617 (US).

PANAMA: Aquarubia, *Killip* 2800 (US); Pecora, *Killip* 2703 (US). CANAL ZONE: Barro Colorado I, *Bailey* 525 (US), Barbour Lathrop Trail, *Wetmore & Woodworth* 150 (GH); betw Frijoles & Monte Lirio, *Killip* 12134 (GH, US); N of Frijoles, *Standley* 27449 (US); Río Indio de Gatún, *Maxon* 4815, 4849 (US). DARIEN: Cana, *Williams* 931 (US). PANAMA: Juan Díaz, *Killip* 2755, 2765 p.p. (US); Charavé River, Chepo, *Pittier* 4721 (US); Pearl Archipelago, Canyon Rd, *Erlanson* 414, 420 (US); Río Merino, *Erlanson* 541 (US); below pumping station, *Johnston* 383 (US), Area M, *Johnston* 71 (US).

BRITISH GUIANA: Kanaku Mts, Mt Iramaikpang, *Smith* 3670 (GH).

VENEZUELA: NUEVA ESPARTA: El Valle, Margarita I, *Miller & Johnston* 163 (GH, MO, US). MIRANDA: Parque Nacional de Guatopo, *Steyermark* 90178 (VEN). BOLÍVAR: El Morrocoy, Guayapo, Bajo Caura, *Williams* 11807 (US); La Unión, Medio Caura, *Williams* 11263 (US).

COLOMBIA: MAGDALENA: Codazzi, *Haught* 3760 (GH, US); Quebrada Soraria, 6 km E of La Jagua, *Haught* 3615 (GH, US); Santa Marta, Río Piedras, *Smith* 1028 (GH, MICH, MO, US). SANTANDER: Barranca Bermeja, Magdalena Valley, betw Sogamoso & Colorado

Rivers, *Haught 1424* (MICH, US). CUNDINAMARCA: Sasaima, *González & Daniel 1885* (US). META: jct of Güejar & Zanza Rivers, *Smith & Idrobo 1499, 1506* (US). CHOCÓ: *Schott 1216* (MO); Lloró, 50 km S of Quibdó, jct of Río Atrato & Río Andágueda, *Archer 2066* (US); S of Río Condoto, betw Quebrada Guarapo & Mandinga, *Killip 35138* (US). VALLE DEL CAUCA: Las Juntas del Dagua, *Lehmann 7668* (US); Río Dagua, Quebrada del Río Blanco, *Cuatrecasas 13671* (US); Río Dagua, betw La Elsa & Río Blanco, *Killip 34734* (US). PERU: LORETO: Río Santiago, above Pongo de Manseriche, *Mexía 6216* (MICH); betw Yurimaguas & Balsapuerto (lower Río Huallaga basin), *Killip & Smith 28164* (US). JUNÍN: Río Pinedo, N of La Merced, *Killip & Smith 23608* (US).

BOLIVIA: COCHABAMBA: Antacahuana, ca 160 km NE of Cochabamba, *Buchtien 2168* (US).

This species is easily recognized by its bright- or gray-green foliage, bright-ferruginous rhizome scales, truncate blades, and silvery pilose pubescence. It varies somewhat from north to south. Material from Central America is smaller, pale- or lime-green, sometimes with a stramineous rachis or costa and more blunt segments. The southern form is larger, more gray-green, and with more acute segments. The hairs of the blade vary in length throughout the range but are always characteristically silvery. Except for pubescence, which is most strongly expressed in the middle of the range (i.e. northern South America), the variation is evidently a cline ranging from smaller, more obtusely lobed plants in Central America to taller, acutely lobed ones in Peru.

The allied species *Polypodium recurvatum* from Paraguay and Brazil differs in being more glabrous and more robust and in having very long, almost acuminate segments, but it is otherwise quite similar. It is isolated geographically from the range of *P. hygrometricum*, and the differences between the two probably result from allopatric speciation.

SPECIES DUBIAE ET EXCLUDENDAE

- Polypodium bolivianum* Rosenst. var. *brevipes* Rosenst., Repert. Sp. Nov. **12**: 473, 1913 (Type: Bolivia, North Yungas, Polo-Polo, nr Corioco, 900 m alt, *Buchtien 3497* S-PA?). This is probably a small specimen of *P. bolivianum* Rosenst.
- P. inversum* Vell., Fl. Flum. **11**: 11, t. 72, 1827, nomen nudum; Arch. Mus. Nac. Rio **5**: 448, 1881. No Velloso types exist; the name must be based on the description and illustration of a plant from Rio de Janeiro, Brazil. It is usually considered a synonym of *P. plumula* (Morton, pers. comm.), but other similar species in that region include *P. dispersum*, *P. siccum* and *P. filicula*.
- P. lomariiforme* Kunze, Linnaea **9**: 42, 1834 (as "*lomariaeforme*") (Type: "in flor. Peruv. montibus aridioribus as Cassapi 1829, Lect. *Diar. 1152*, Herb. Poepp., Kze., etc."). I have seen a specimen at K labeled as having been sent to Kunze from Poeppig. It is dated 1830, but Mr. Morton (pers. comm.) indicates that Poeppig's Peruvian collections are often misdated. Kunze's herbarium at Leipzig is destroyed. The Kew specimen may be an isotype although Dr. Jarrett questions this (pers. comm.). There may be authentic material at Berlin. The specimen agrees with the protologue except that the frond is pinnatisect rather than pinnate, and it agrees with my *P. camptophyllum* Fée var. *lachniferum* (Hier.) Evans. If a satisfactory determination of type material supports this, *P. lomariiforme* would take precedence.

- P. maenurum* Link, Hort. Reg. Bot. Berol. Descr. **2**: 96, 1833 (Type: none cited, probably at B). The protologue compares it to *P. paradiseae* Langsd. & Fisch., and it has been considered a synonym of *P. recurvatum*.
- P. otites* L., Sp. Pl. 1085, 1753 (Type: none in LINN; based on the illustration in Petiver, Pteridographia 32, t. 1, fig. 16). Although this name has been associated with *P. pectinatum* L., it is not a member of this complex, and is more nearly allied with *P. tenuifolium* Humb. & Bonpl. ex Willd. [in L., Sp. Pl., ed. 4, **5**: 185, 1810 (Type: Venezuela, Cumanacoa, *Humboldt* 437 B-photo)].
- P. pectinatiforme* var. *brevipes* Rosenst. in Buchtien, Contrib. Fl. Bolivia **1**: 38, 1910, nomen nudum.
- P. pectinatiforme* f. *parvum* Sehnen, Pesquisas, Bot. **10**: 33, 1960. No type is cited and the name is, therefore, invalidly published.
- P. pectinatum* var. *acuminatum* Baker, Jour. Bot. Brit. For. **25**: 25, 1887 (Type: Costa Rica, Cooper K). The specimen is incomplete and cannot be determined with confidence. It appears not to belong to this complex.
- P. pectinatum* L. var. *baezanum* Mille, Revista Col. Nac. Vic. Rocofuerte **9**: 202, 1927 (Type: none cited; authentic material may be at B or in Ecuador). It is not possible to place this name with confidence; it may be *P. consimile* Mett.
- P. pectinatum* L. var. *bourgaeum* Fourn., Mex. Pl. 76, 1872. (Syntypes: "In valle Cordobensi, dec. sp. *Bourgeau* 1431, 1436; Guadalupe, Nova-Grenada *Lindig* 45; Brasilia."). No syntype has been seen, but the protologue indicates that the plant has ellipsoid sori and anastomosing veins, neither of which would place it in *P. pectinatum* L., and would tend to exclude it from the group altogether.
- P. pectinatum* L. var. *brachypus* Sodiro, Crypt. Vasc. Quit. 334, 1893 (Type: "Crece en los bosques de Gualea colectado por el Sr. D. Rodolfo Riofrio."). No type has been seen; the description is inconclusive.
- P. pectinatum* L. var. *hispidum* Christ in Pittier, Prim. Fl. Cost. 3: 15, 1901 (as "*hispidum*") (Type: "El Paramó, 3000 m, versant E du massif de Buena Vista, Jan 1897, *Pittier* 10474 P? or BR?). = *Ctenopteris semihirsuta* (Klotzch) Copeland, Phil. Jour. Sci. **84**: 450, 1955).
- P. pectinatum* L. var. *jürgensii* Rosenst., Hedwigia **43**: 229, 1904 (Syntypes: Brazil, Santa Cruz, auf Berg João Rodriquez, 200 m, *Jürgens & Stier* 82 S-PA?; Joinville, Santa Catharina, *Schmalz* 56 S-PA?). *Schmalz* 56 at MO is not a member of this complex, and other material has not been seen.
- P. pectinatum* L. var. *paradisiae* Sodiro, Crypt. Vasc. Quit. 334. 1893, non Baker, 1870 (Type: "Crece en la region tropical y subtropical, en lugares secos y pedregosos; en la orilla del rio Pilatón."). This is presumed to be a new variety rather than a transfer as *P. paradiseae* Langsd. & Fisch. is cited only with a query, and does not occur in Ecuador. From the description, *P. bolivianum* suggests itself.
- P. venustum* Desv., Gesell. Naturf. Freund. Berlin Mag. **5**: 315, 1811 (Type: "Habitat in America calidiore Antillisque", Herb. Desv. P-photo). Although Christensen (1906) referred this name to *P. taxifolium* L., the photo of the

type indicates that it is a eupolypodium. It would appear to be *P. camptophylarium* Fée, over which it would take precedence, but I would have to see the specimen to be sure that it was not *P. eurybasis* or *P. consimile*.

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Fig. 1. Morphology of the sporophyte. (A) Rhizome cross-section of *P. ptilodon* var. *robustum*, de la Sota 10 (EVANS), $\times 5.5$. (B) Vascular bundle from A, $\times 80$. (C) Rhizome cross-section of *P. truncorum*, de la Sota 21 (EVANS), showing only two vascular bundles and thick-walled cells of the inner ground parenchyma, $\times 5.5$. (D) Cross-section of the blade segment of *P. ptilodon* var. *robustum*, de la Sota 10 (EVANS), showing the mesophyll and the sclerified bundle sheath, $\times 80$. (E) Localized distribution of laminar hairs around the sorus in *P. ptilodon* var. *ptilodon*, Hutchison 1470 (MICH), $\times 6.5$. (F) Ctenoid hairs of the rachis of *P. ptilodon* var. *ptilodon*, Hutchison 1470 (MICH), $\times 6.5$. (G) Rhizome palea of *P. dispersum*, Evans 2007 (MICH), $\times 18$. (H) Rachis palea of *P. dispersum*, Evans 2007 (MICH), $\times 18$. (I) Rhizome palea of *P. cupreolepis*, Pringle-3353 (GH), $\times 18$. (J) Rhizome palea of *P. plumula*, Copeland 16059 (MICH), $\times 18$. (K) Palea from the rhizome apex of *P. bolivianum*, (US 1007896), $\times 18$. (L) Palea from the side of the rhizome of *P. bolivianum*, (US 675781), $\times 18$.

Fig. 2. Gametophyte development and sporophyte juvenile leaves. (A) Stages of development of the young gametophyte of *P. dispersum*, Evans 2008 (MICH). (B) Stomates on the gametophyte of *P. dispersum*, Evans 2008 (MICH). (C) Stages of development of the young gametophyte of *P. ptilodon* var. *caespitosum*, Evans 2002 (MICH). (D) Mature gametophytes and heteroblastic leaf series of juvenile leaves of *P. dispersum*, Evans 2008 (MICH). (E) Heteroblastic series of juvenile leaves of *P. plumula*, Evans 1187 (MICH). (F) Mature gametophytes and heteroblastic leaf series of juvenile leaves of *P. ptilodon* var. *caespitosum*, Evans 2005 (MICH).

Fig. 3. Representative frond shapes. (A) *P. ptilodon* var. *robustum*, Pabst s.n. (MICH). (B) *P. paradiseae*, Sehnen 2 (MICH). (C) *P. curvans*, Stork, et al., 10626 (MO). (D) *P. truncorum*, Pabst s.n. (MICH). (E) *P. dispersum*, Evans 2008 (MICH). (F) *P. plumula*, Evans 1187 (MICH). (G) *P. recurvatum*, Sehnen 4 (MICH).

Fig. 4. Epidermal cells, hairs and paraphyses of the lamina. Fig. A-G, Epidermal cells. (A) *P. dispersum* (US 1287974). (B) *P. filicula* (US 1280298). (C) *P. sicum*, (US 1516124). (D) *P. truncorum*, Mexia 5105 (GH). (E) *P. hygrometricum*, Chrysler & Roever 5318 (MICH). (F) *P. absidatum* (US 1833997). (G) *P. camptophyllum* var. *macedoi* (US 2081770). (H) Transition of costal hairs to costal paleae in *P. plumula* (US 1049810). (I) Variation in the ctenoid hairs of *P. ptilodon* var. *caespitosum*, McFarlin s.n., Nov. 4, 1930 (MICH): 1. Rachis; 2. Costa; 3. Lamina; 4. Receptacular paraphyses. Fig. J-P, Laminar hairs and paraphyses. (J) *P. dispersum*: 1. Capsular and receptacular paraphyses, Wagner 62061 (MICH); 2. Clavate hairs of the costa and lamina (US 1287974); 3. Acicular hairs of the abaxial surface of the costa (US 1287974). (K) *P. filicula*: 1. Receptacular paraphyses, Ahmuda & de la Sota 51 (EVANS); 2. Clavate hairs of the abaxial surface of the lamina (US 1280298); 3. Acicular hairs of the segment margin (US 1280298); 4. Acicular hairs of the abaxial surface of the costa (US 1280298). (L) *P. absidatum* (US 1833997): 1. Capsular setae; 2. Clavate hairs of the lamina; 3. Hairs of the abaxial surface of the costa; (M) *P. camptophyllum* var. *macedoi* (US 2081770): 1. Clavate, short and long acicular and setose-clavate forked hairs of the lamina; 2. Acicular hairs of the segment margin; 3. Acicular hairs of the abaxial surface of the costa; 4. Capsular setae and receptacular paraphyses. (N) *P. venturii*, Venturi 2970 (GH): 1. (Receptacular paraphyses; 2. Clavate and acicular laminar hairs. (O) *P. ptilodon* var. *robustum*, de la Sota & Cuzzo 1556 (EVANS), Capsular seta and simple and branched receptacular paraphyses. (P) *P. sursumcurrens*, Copeland 128 (MICH): 1. Clavate laminar hairs; 2. Receptacular paraphyses, showing the range from the simple hair to those with a multicellular subterminal expansion.

Fig. 5. Representative types of rachis paleae. (A) *P. plumula* from: 1. Jamaica, Maxon et al. 1234 (GH); 2. Mexico Copeland 16055 (MICH); 3. Mexico (US 1745606); 4. Panama, Taylor 1390 (MICH); 5. Colombia (US 1692356); 6. Peru (US 2356738); 7. Brazil (US 762365). (B) *P. dispersum*, Evans 2007 (MICH). (C) *P. atrum*, Lundell 6639 (US). (D) *P. bermudianum*, Brown 464 (GH). (E) *P. singeri*, Ahmuda & de la Sota 53 (EVANS). (F) *P. ferrugineum*, Copeland 125 (MICH). (G) *P. cupreolepis*, Pringle 3353 (GH). (H) *P. ptilodon* var. *caespitosum* (FLAS-P1718). (I) *P. filicula*, Ahmuda & de la Sota 51 (EVANS). (J) *P. dispersum* (FLAS-P1155, FLAS-P4879). (K) *P. ptilodon* var. *caespitosum* (FLAS-P4881). (L) *P. plumula* (FLAS-P1153, FLAS-P5166).

Fig. 6. Venation patterns and segment shapes. Most of the segments lack the expanded basal portion, M and N lack medial portions, and O and S_1 lack terminal portions. (A) *P. truncorum*, Mexía 5105 (GH). (B) *P. siccum* (US 1516124). (C) *P. filicula* (US 1280298). (D) *P. cupreolepis*, Pringle 3353 (GH). (E) *P. sursumcurrens*, Copeland 128 (GH). (F) *P. bermudianum* (sterile segment with portion of a fertile segment) (US 848332). (G) *P. dispersum*, Evans 2007 (MICH). (H) *P. hygrometricum*, Chrysler & Roever 5318 (MICH). (I) *P. plumula*, Maguire 25005 (GH). (J) *P. atrum*, Stoutamire 3563 (MICH). (K) *P. ptilodon* var. *caespitosum*, McFarlin s.n., 4 Nov. 1930 (MICH). (L) *P. pectinatiforme*, Copeland 13601 (MICH). (M) *P. bolivianum* (US 675781). (N) *P. consimile* var. *pastazense* (US 2254236). (O) *P. recurvatum*, Copeland 21561 (MICH). (P) *P. venturii*, Venturi 2974 (GH). (Q) *P. camptophyllum* var. *macedoi* (US 1081770). (R_1) *P. pectinatum*, from Guadeloupe (US 1712313). (R_2) *P. pectinatum*, from Surinam. (S_1) *P. camptophyllum* var. *camptophyllum*, from Haiti, with typical venation pattern (US 1783820). (S_2) *P. camptophyllum* var. *camptophyllum*, from Bolivia, with extreme venation pattern (US 1191631). (T) *P. choquetangense*, Cárdenas 3161 (MICH).

Fig. 7. Habitat studies. (A) *P. dispersum*, on mossy sandy soil, Evans 1189 (MICH), $\times \frac{1}{12}$. (B) *P. plumula*, on *Quercus virginianum* trunk, Evans 1187 (MICH), $\times \frac{1}{12}$. (C) *P. dispersum*, small proliferations from an exposed root mass, Evans 1189 (MICH), $\times \frac{4}{5}$. (D) *P. singeri*, short rhizomes probably originating as root proliferations along a small twig, arrows mark the individual rhizomes, Gerdez 54 (S-PA), $\times \frac{1}{6}$. (E) *P. ptilodon* var. *caespitosum*, growing on a rotten log, Evans 2004 (MICH), $\times \frac{1}{12}$. (F) *P. dispersum*, root proliferations from a root growing through the hole in the bottom of the pot, the youngest proliferation is marked with an arrow, Evans 1130 (MICH), $\times \frac{1}{12}$. (G) *P. dispersum*, colony made up entirely of small non-soriferous plants, presumed to have originated entirely from root proliferations, Evans 2016 (MICH), $\times \frac{1}{24}$.

Fig. 8. Geographic distribution of species in the *Polypodium pectinatum-plumula* complex, (as represented by herbarium specimens). (A) Geographic distribution of *P. ferrugineum*, *P. hygrometricum*, *P. recurvatum*. (B) Overall distribution of the species of the complex; major and marginal areas are distinguished according to the key on the map. (C) Geographic distribution of *P. bolivianum*, *P. consimile* var. *consimile* & var. *pastazense*, *P. singeri*. (D) The five areas of distribution of the individual species of the complex as indicated by the key accompanying the map.

Fig. 9. Geographic distribution of species in the *Polypodium pectinatum-plumula* complex, (as represented by herbarium specimens). (A) *P. plumula*, *P. sursumcurrens*. (B) *P. atrum*, *P. dispersum*, *P. filicula*.

Fig. 10. Geographic distribution of species in the *Polypodium pectinatum-plumula* complex, (as represented by herbarium specimens). (A) *P. alfredii*, *P. paradiseae*, *P. pectinatiforme*, *P. pectinatum*, *P. venturii*. (B) *P. camptophyllum* var. *abbreviatum*, var. *camptophyllum*, var. *lachniferum* & var. *macedoi*, *P. cupreolepis*, *P. siccum*.

Fig. 11. Geographic distribution of species in the *Polypodium pectinatum-plumula* complex, (as represented by herbarium specimens). (A) *P. ptilodon* var. *caespitosum*, var. *pilosum*, var. *ptilodon*, var. *robustum*. (B) *P. absidatum*, *P. choquetangense*, *P. curvans*, *P. eurybasis* var. *eurybasis*, var. *glabrescens* & var. *villosum*, *P. truncorum*.

Fig. 12. Stages of sporogenesis in *Polypodium ptilodon* var. *caespitosum*, Evans 1157 (MICH). (A) Cytokinesis in the 8 pre-mother cells, $\times 160$. (B) 16 spore mother cells, $\times 160$. (C) Meiosis in the 16 spore mother cells, $\times 130$. (D) 74 pairs of chromosomes at meiotic metaphase in a spore mother cell, $\times 760$. (E) Young spore tetrads with four nuclei, before cytokinesis, $\times 160$. (F) Young tetrads during cytokinesis, $\times 240$. (G) Young tetraspores, $\times 240$. (H) Mature spores, showing long-reniform shape and tuberculate surface, $\times 760$.

Fig. 13. Stages in sporogenesis in *Polypodium dispersum*, Wagner 62061 (MICH). (A) Mitosis in the eight pre-mother cells, $\times 160$. (B) Cytokinesis in the eight pre-mother cells, $\times 160$. (C) 16 spore mother cells, $\times 160$. (D) Mitosis in the 16 spore mother cells, $\times 160$. (E) 111 univalent chromosomes at metaphase in the spore mother cells, $\times 760$. (F) Cytokinesis in the 16 diads of young diplospores, $\times 160$. (G) Mature spores, one without a scar, the other with a monolete scar, $\times 760$. (H) 32 young diplospores, $\times 160$.

Fig. 14. Variation in the scar configuration of spores of *Polypodium dispersum*, Wagner 62061 (MICH), Proctor 22896 (MICH).

Fig. 15. Gametophyte of *Polypodium dispersum*, Evans 2008 (MICH). (A) Germinating spore, $\times 120$. (B) Formation of the cell plate and branching of the thallus, $\times 120$. (C) Young apogamous sporophytes proliferating from gametophytes on agar plates, several sporophytes are indicated by arrows, $\times 4$. (D) Two-and-one-half-month-old gametophytes showing a portion of an apogamous sporophyte and the position of stomates on the gametophyte (marked with an arrow), $\times 24$. (E) Three stomates from gametophyte in D, $\times 120$. (F) Young apogamous sporophyte showing simple and branched clavate hairs, $\times 50$. (G) Young apogamous sporophyte from small elliptical gametophyte, $\times 20$.

Fig. 16. Specialization in the *Polypodium pectinatum-plumula* complex. (A) Rhizome long-creeping (0) to short-creeping or erect (1); (B) Rhizome paleae narrowly triangular (0) to cordate (1); (C) Rhizome paleae non-comose (0) to comose (1) to comose hairs completely obscuring the paleae (2.5); (D) Rachis brown (0) to black (1); (E) Rachis stiff (0) to elastic (1); (F) Rachis straight (0) to spiralled or circinate (1); (G) Rachis glabrous or thinly pilose (0) to densely villose (1); (H) Ctenoid hairs absent (0) to present (1); (I) Rachis paleae filiform (0) to non-filiform (1); (J) Fronds generally 25 cm to 150 cm (0) to less than 25 cm (1); (K) Frond stipitate (0) to sessile (1); (L) Base of the blade subtruncate or cuneate (0) to definitely truncate (1); (M) Basal segments perpendicular to the rachis (0) to occasionally deflexed (0.5) to regularly deflexed (1); (N) Segments perpendicular to the rachis (0) to ascending (1); (O) Perpendicular segment base symmetrical (0) to asymmetrical when the segment is perpendicular to the rachis (1); (P) Segment margin entire (0) to crenate (1) to pinnatifid (1.5); (Q) Lamina glabrous (0) to pubescent (1); (R) Pubescence evenly distributed (0) to localized (1); (S) Lateral veinlets forked (0) to simple (1); (T) Sori medial (0) to marginal (1); (U) Receptacular paraphyses simple (occasionally forked) and with uniform cells (0) to: U_1 paraphyses with a subterminal irregular multicellular expansion (1) or: U_2 paraphyses regularly branched—one branch tipped with a clavate cell and the other tipped with a setose cell (1); (V) Spores up to 50 μ long (0) to over 50 μ long (1); (W) Spores 64 per sporangium (0) to 32 per sporangium (1).

Solid dots represent extant taxa; hollow dots represent hypothetical ancestral intermediates. The character letter is given the first time the specialized condition appears in an evolutionary line. Small letters represent intermediate character states (0.5); capital letters followed by an apostrophe (') represent an extreme character state (1.5). The dotted lines leading to *P. dispersum* indicate its hybrid nature and probable parental types.

Fig. 17. Type specimens of new taxa. Left. *P. cupreolepis* A. M. Evans, Pringle 3353 (US 66004). Right. *P. bermudianum* A. M. Evans, Brown 464 (US 84332), $\times 1/4$.

Fig. 18. Type specimens of new taxa. Left. *P. atrum* A. M. Evans, Lundell 6639 (US 1638286). Right. *P. camptophyllum* var. *abbreviatum* A. M. Evans, Herrera 872 (US 1342112), $\times 1/4$.

Fig. 19. Type specimens of new taxa. Left. *P. eurybasis* var. *villosum* A. M. Evans, Fosberg 19688 (US 2290492). Right. *P. ptilodon* var. *pilosum* A. M. Evans, Jenman s.n., in 1897 (NY), $\times 1/4$.

Fig. 20. Type and representative specimens. Left. Type of *P. absidatum* A. M. Evans, Killip & Smith 18518 (US 1353919). Right. Representative specimen of *P. pectinatum* L. s.s., Evans 2587 (TENN), $\times 1/4$.

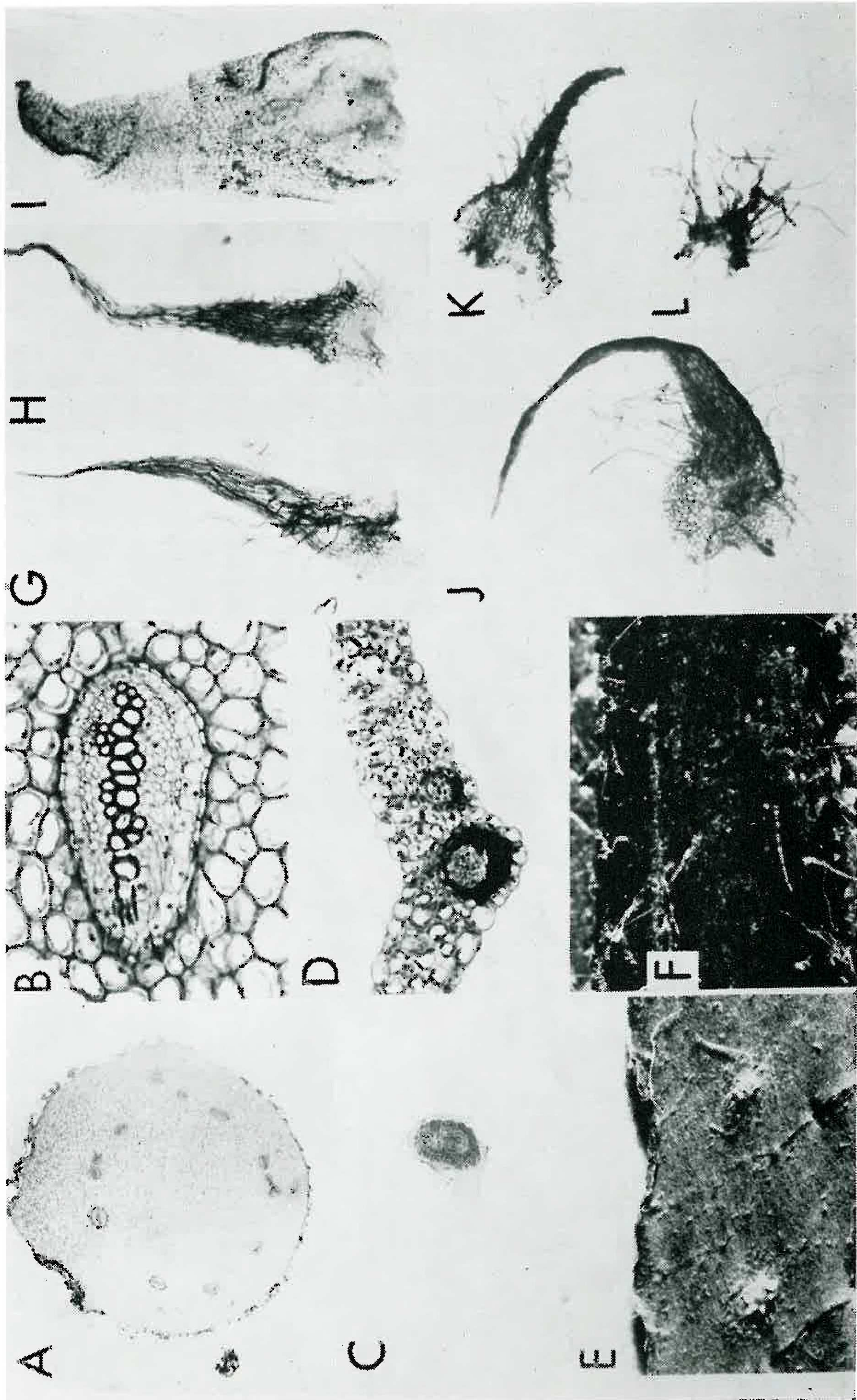


Fig. 1. Morphology of the sporophyte (legend p. 269).

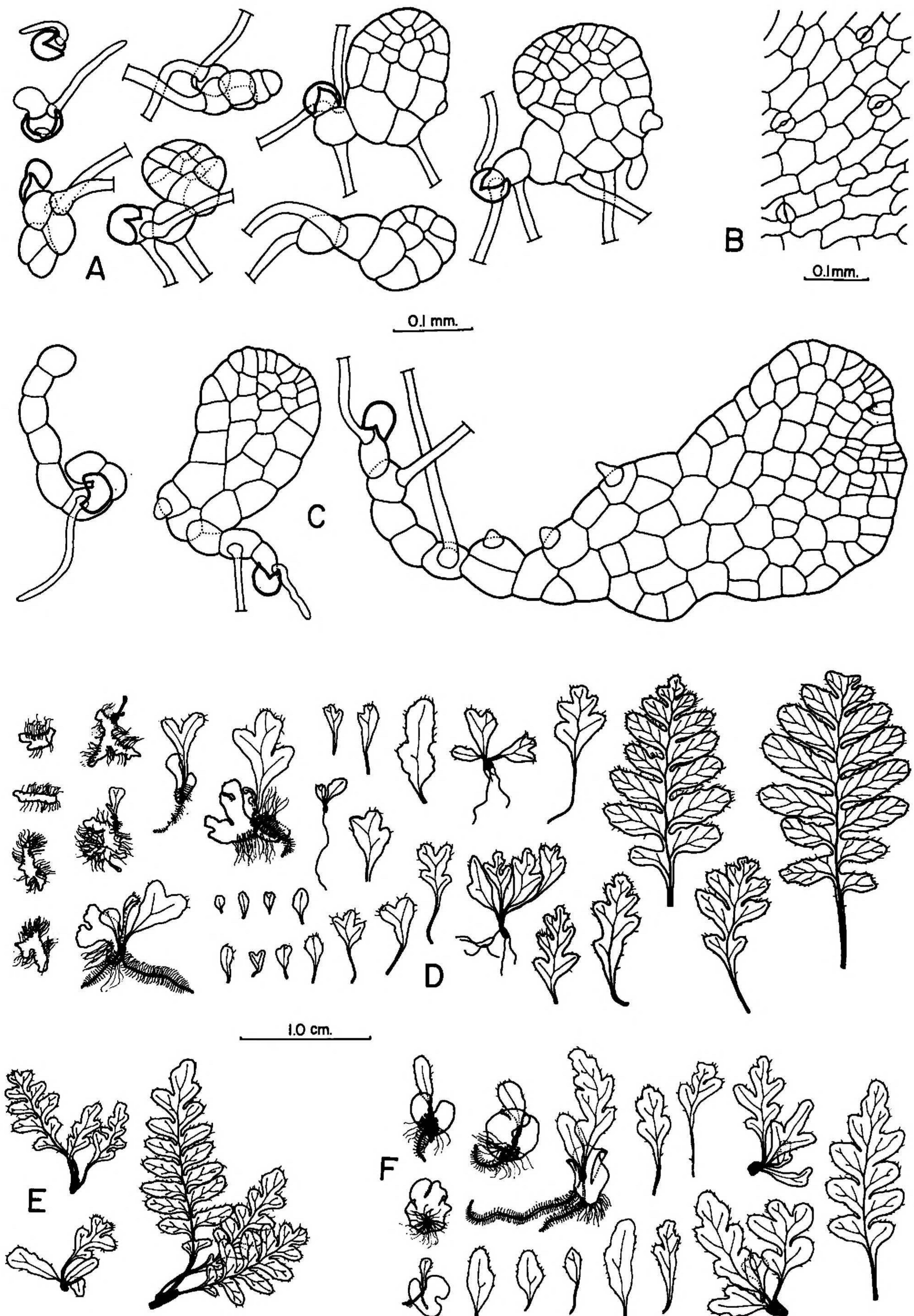


Fig. 2. Gametophyte development and sporophyte juvenile leaves (legend p. 269).

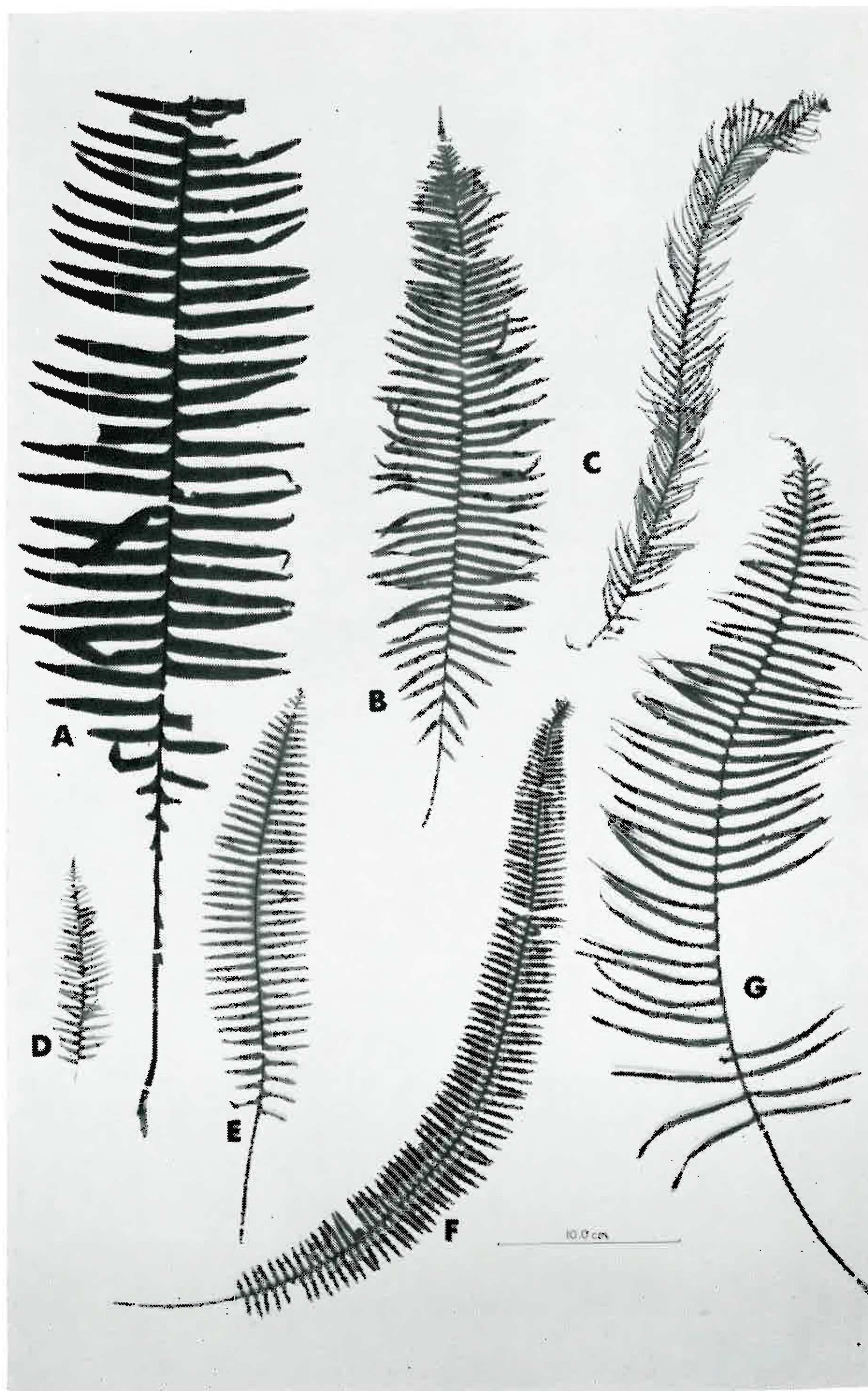


Fig. 3. Representative frond shapes (legend p. 269).

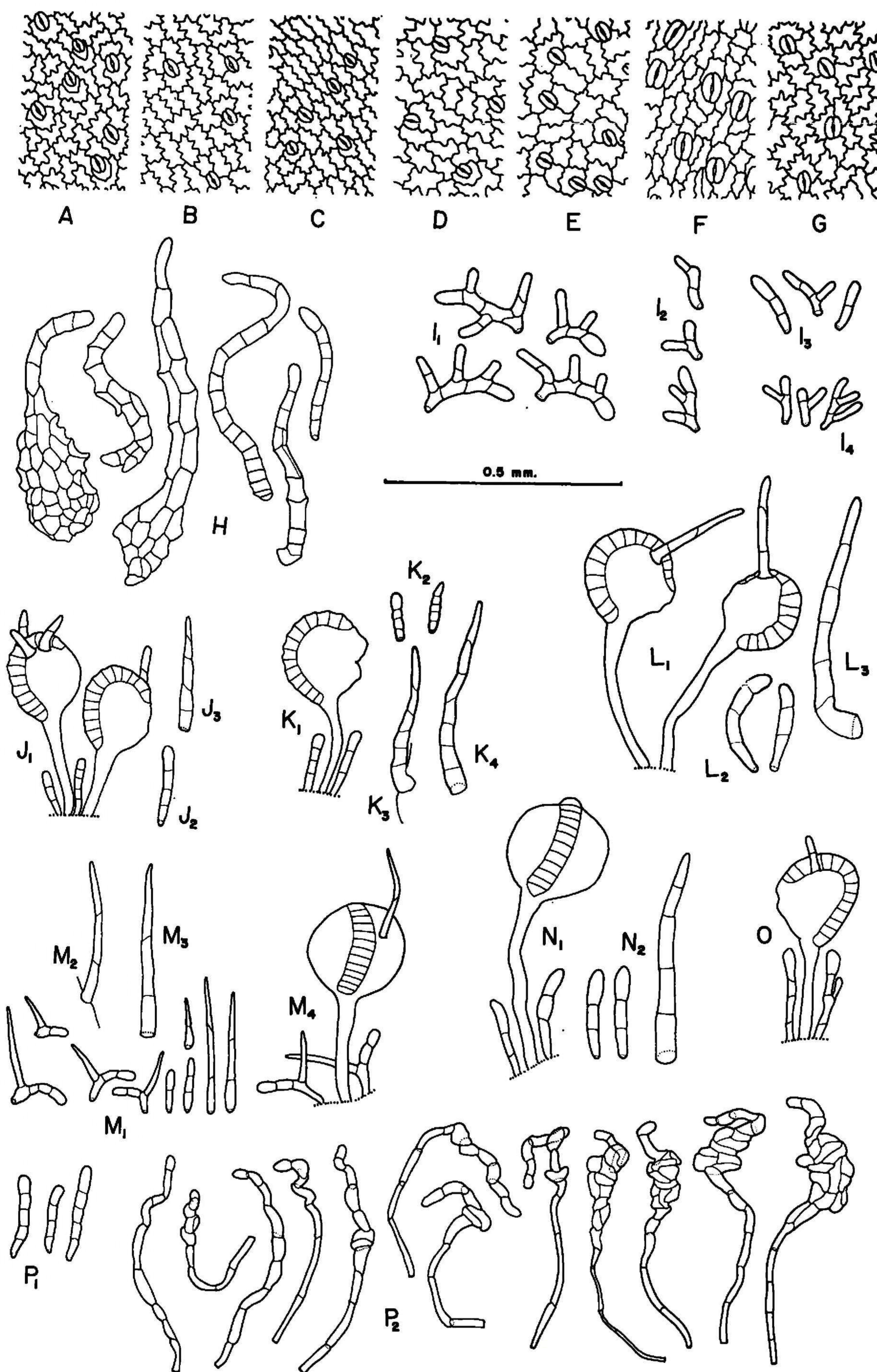


Fig. 4. Epidermal cells, hairs and paraphyses of the lamina (legend p. 269).

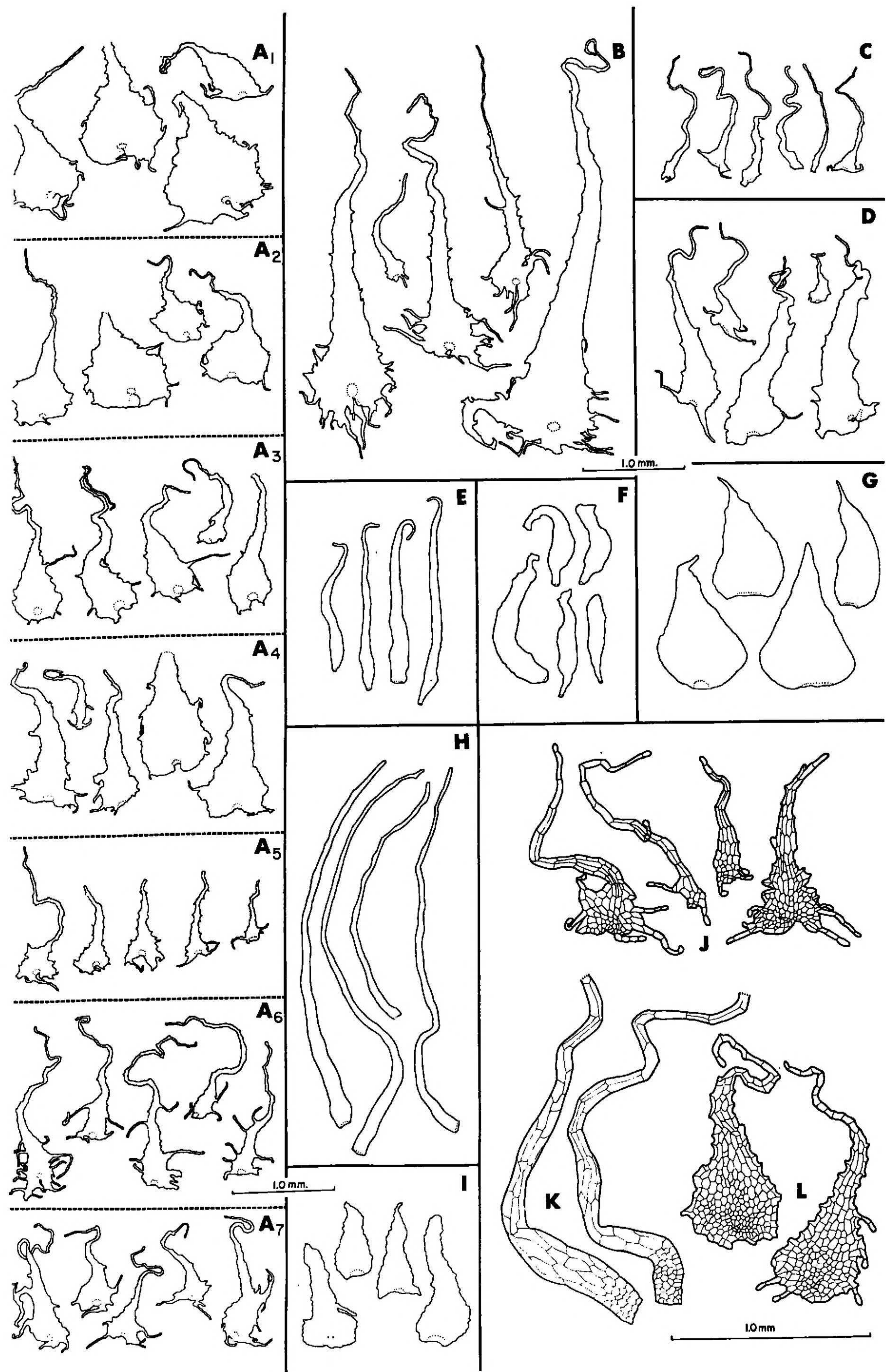


Fig. 5. Representative types of rachis paleae (legend p. 269).

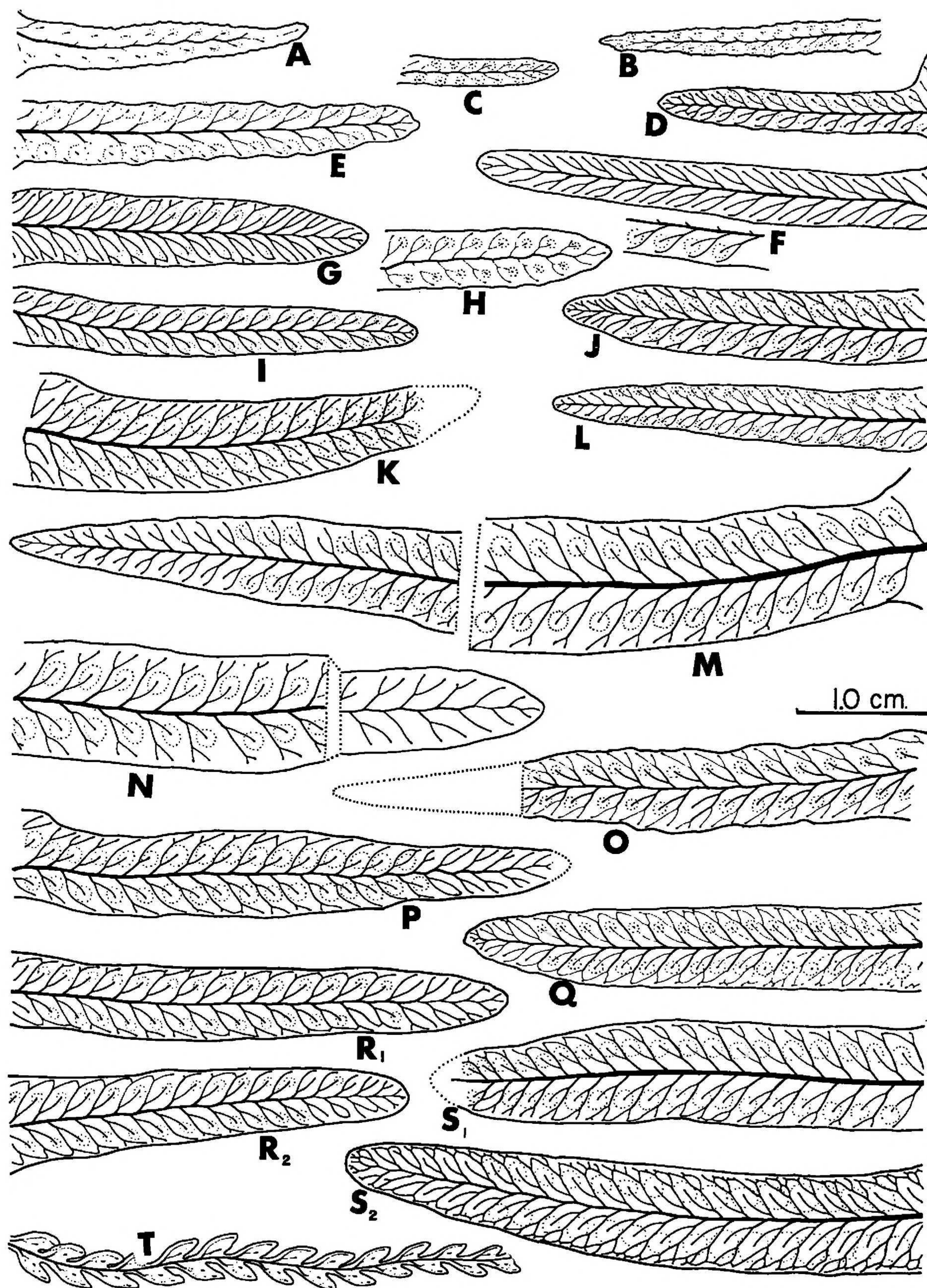


Fig. 6. Venation patterns and segment shapes (legend p. 270).

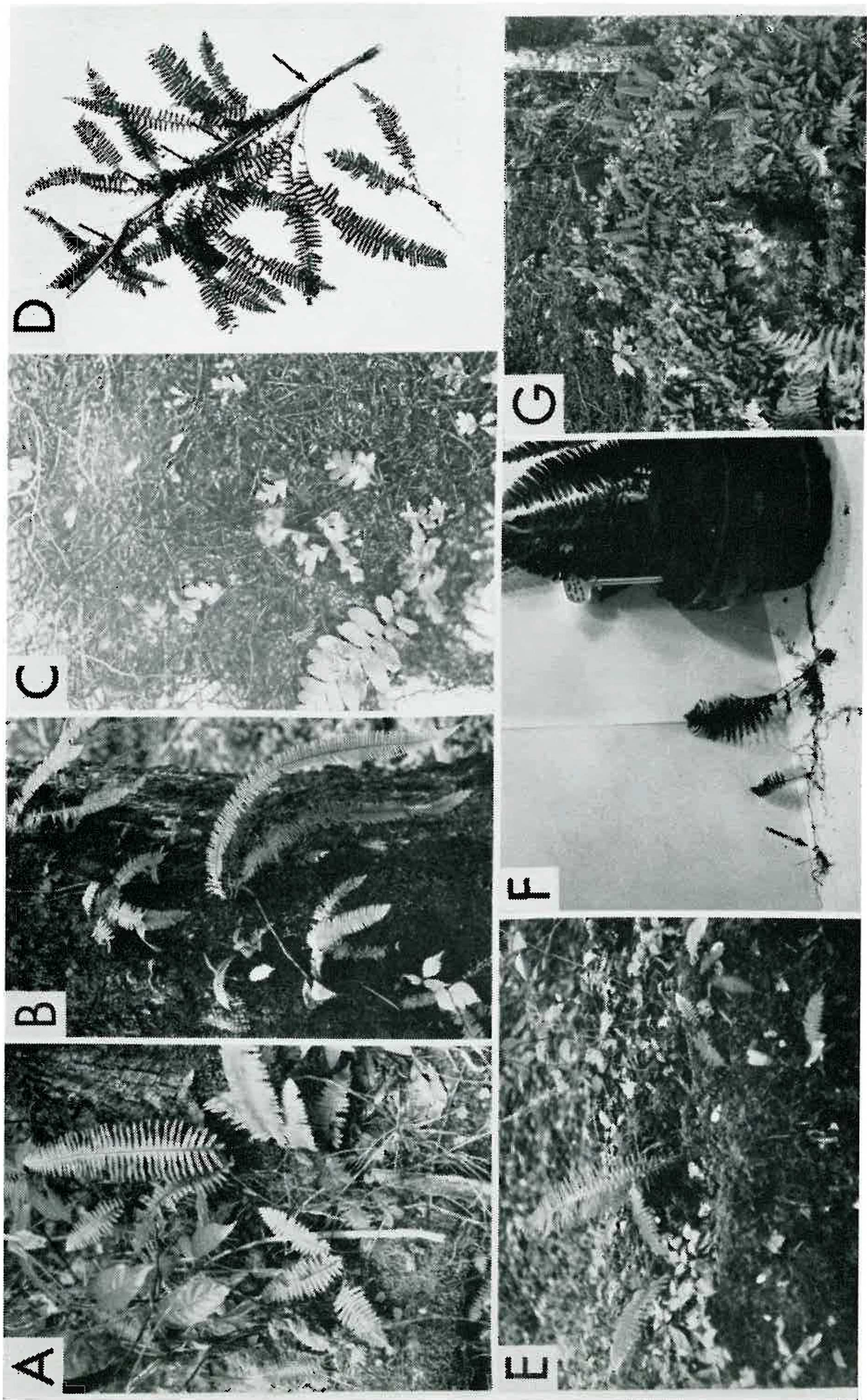


Fig. 7. Habitat studies (legend p. 270).

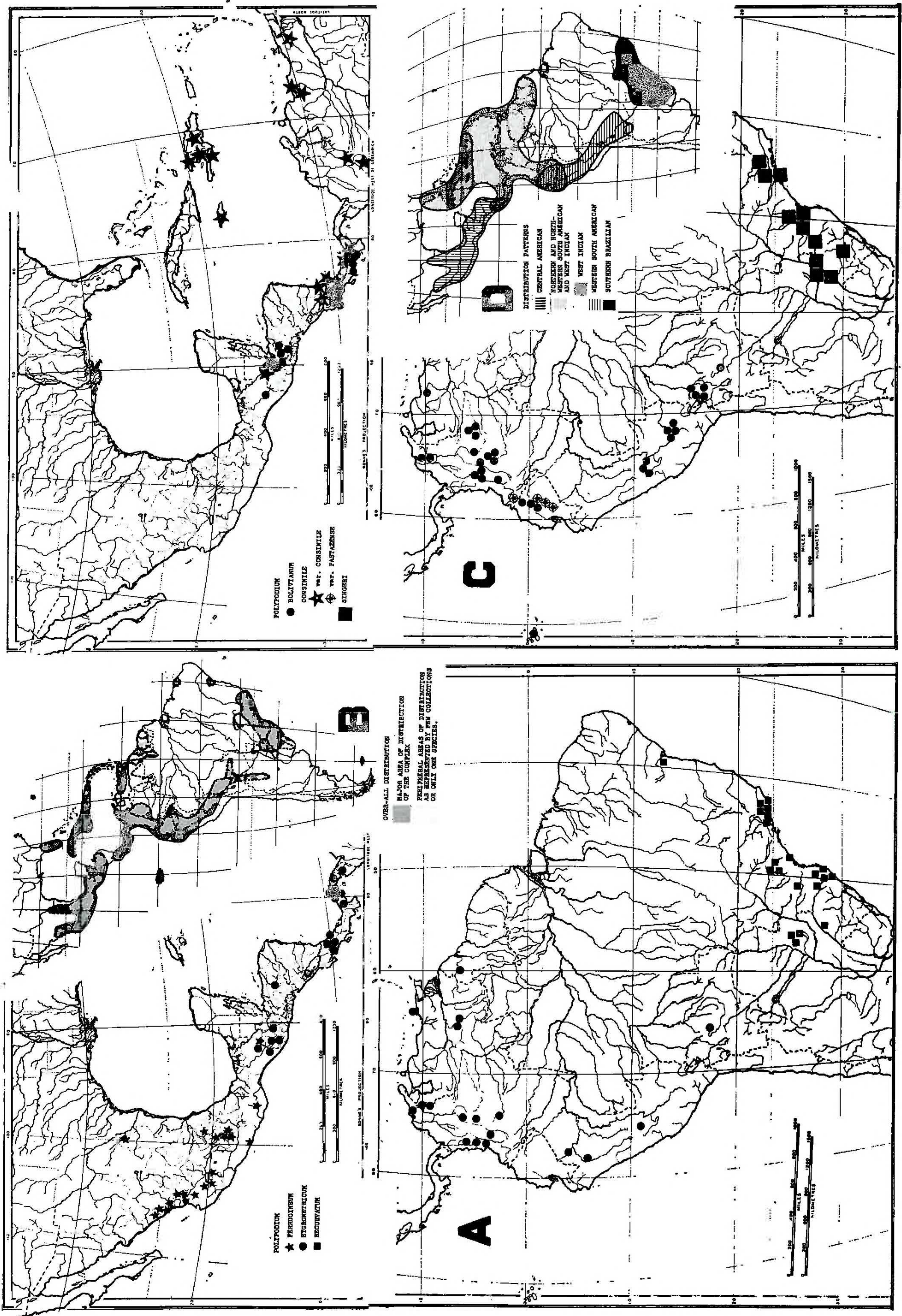


Fig. 8. Geographic distributions (legend p. 270).

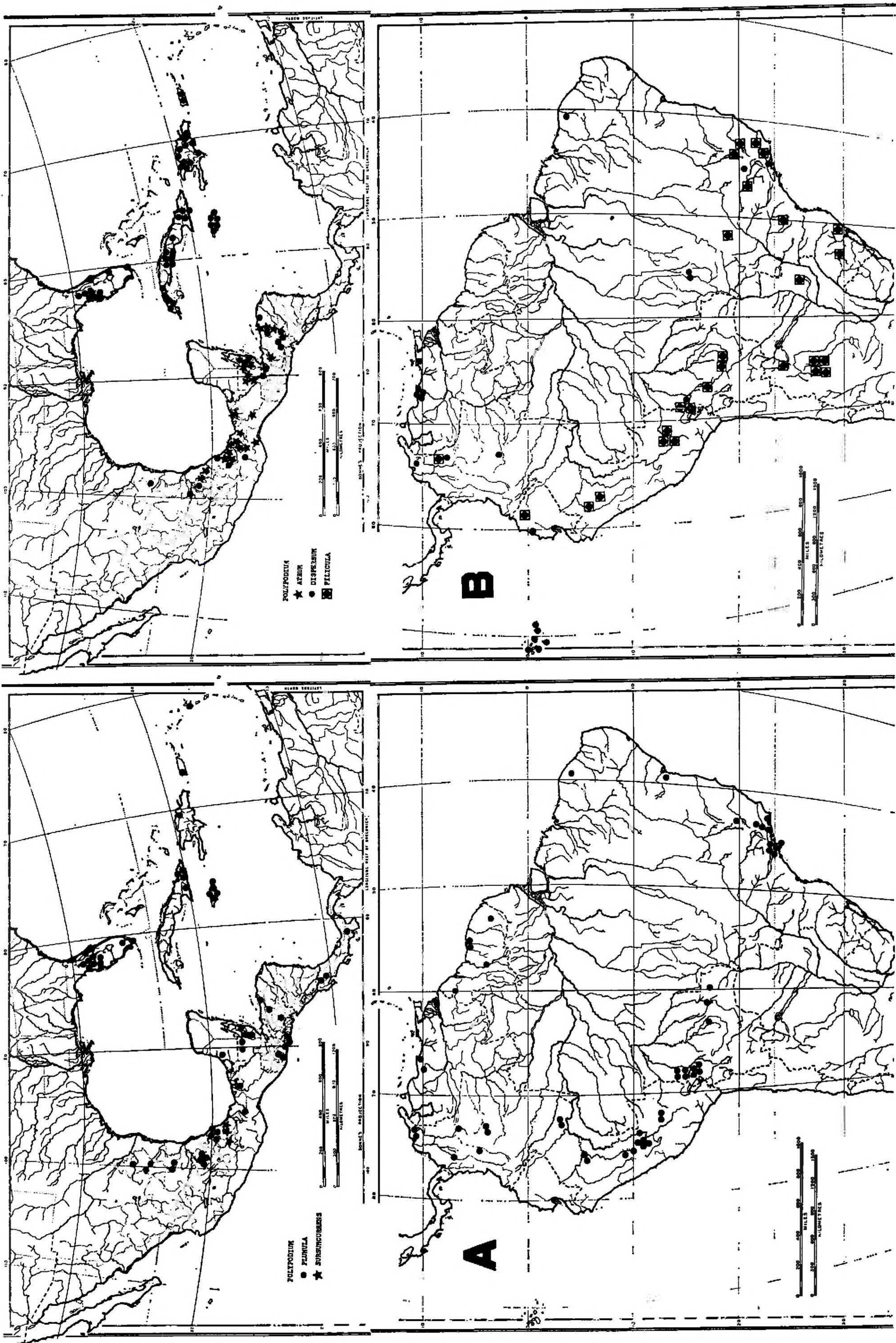


Fig. 9. Geographic distributions (legend p. 270).

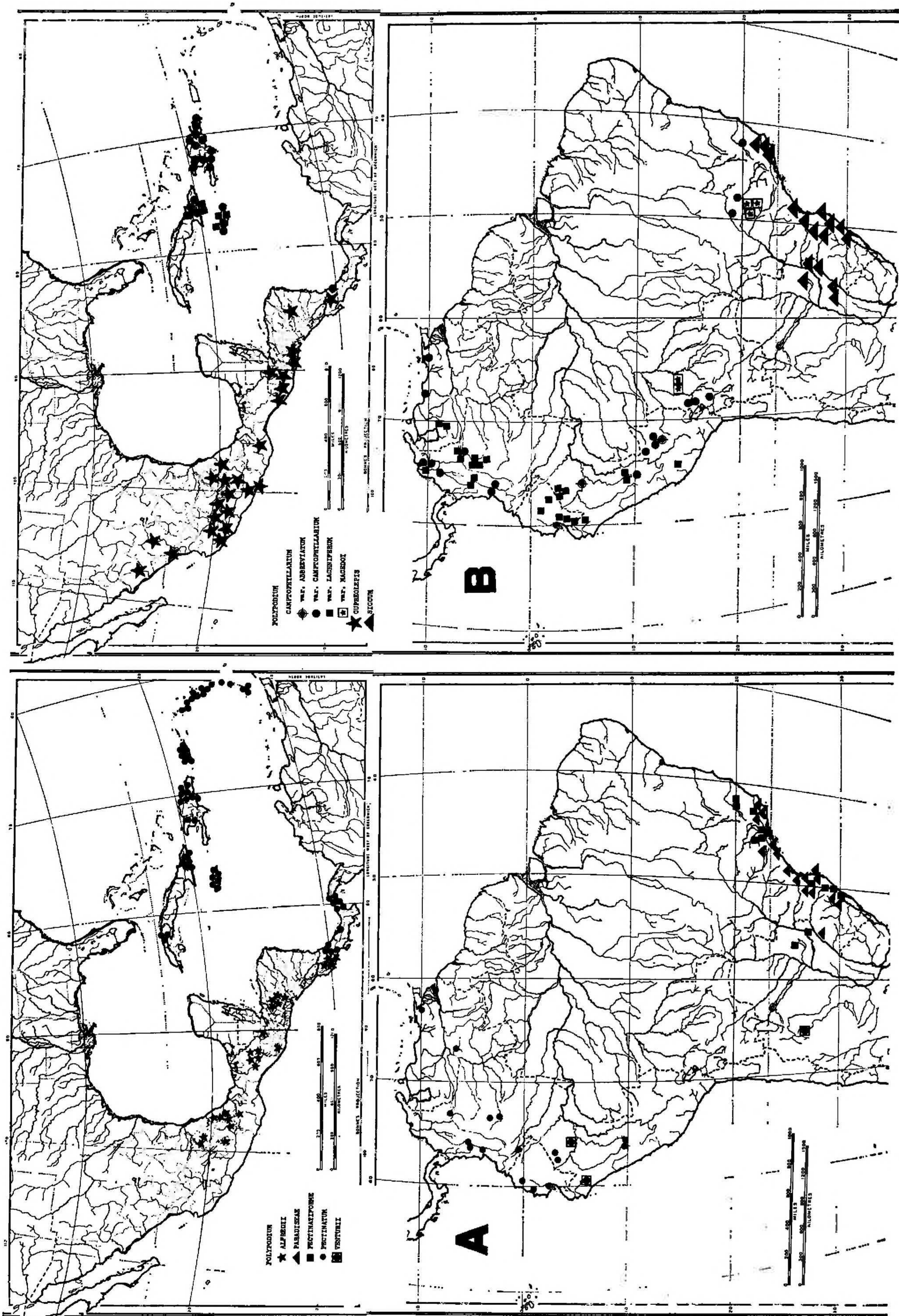


Fig. 10. Geographic distributions (legend p. 270).

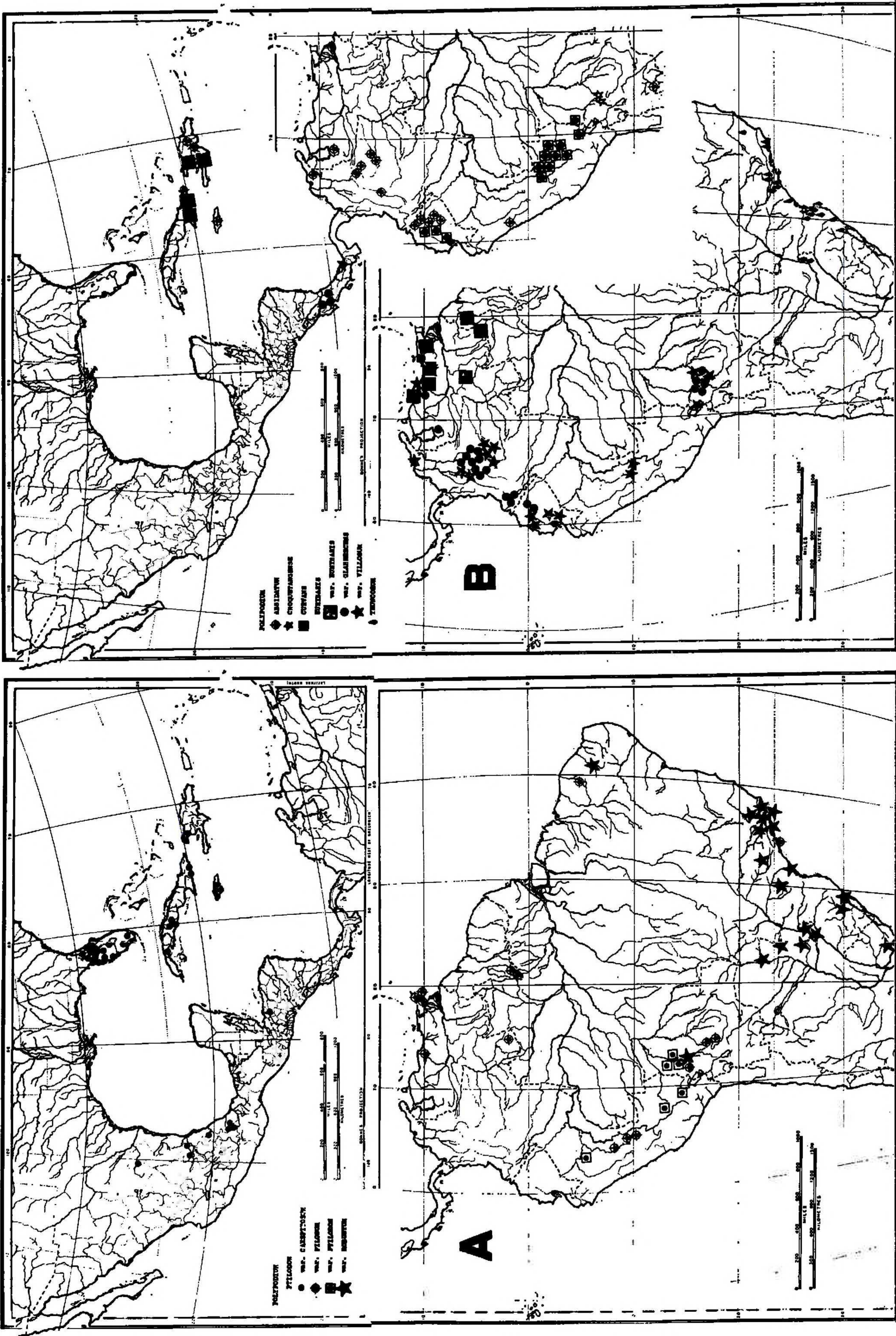


Fig. 11. Geographic distributions (legend p. 270).

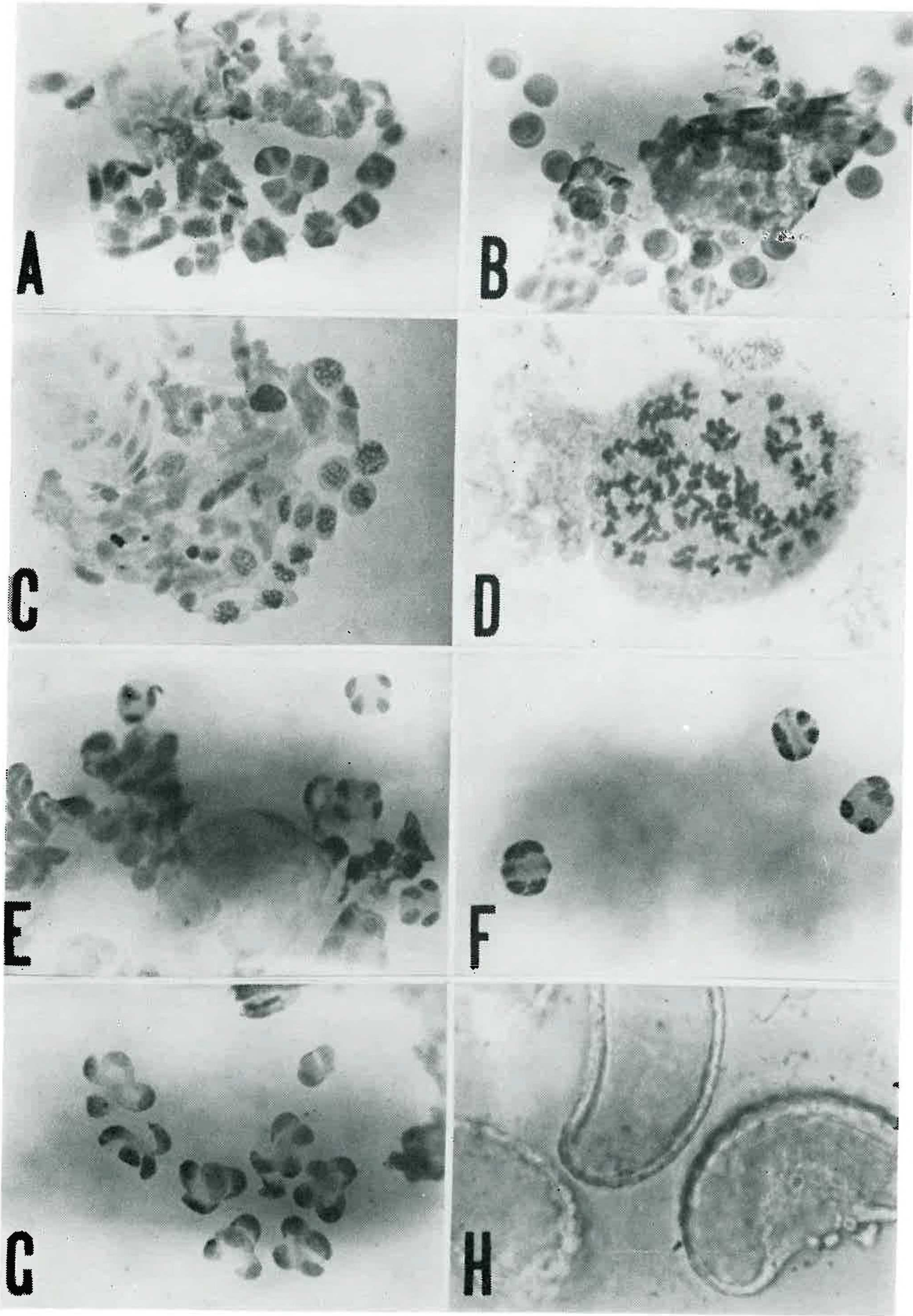


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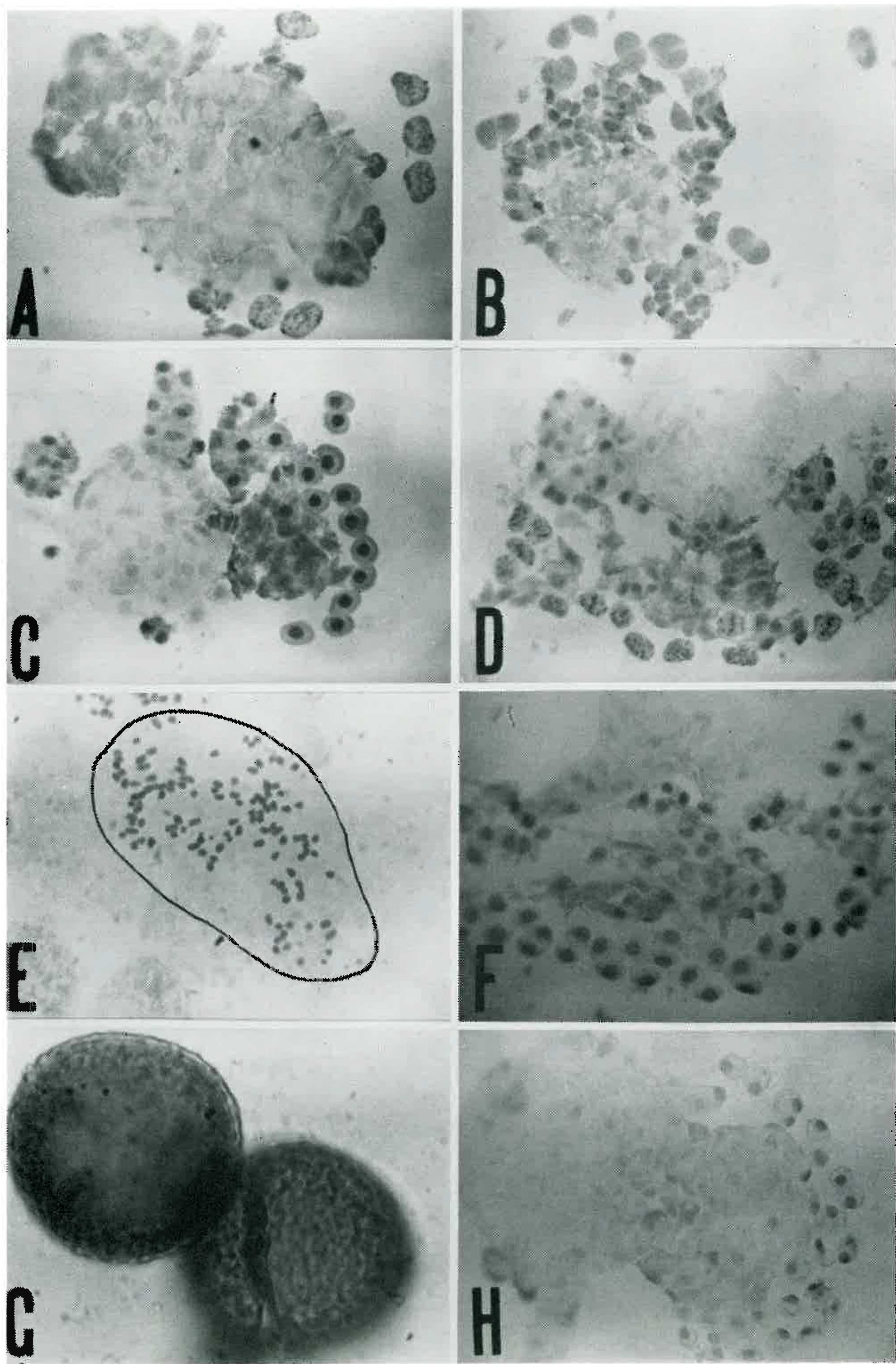


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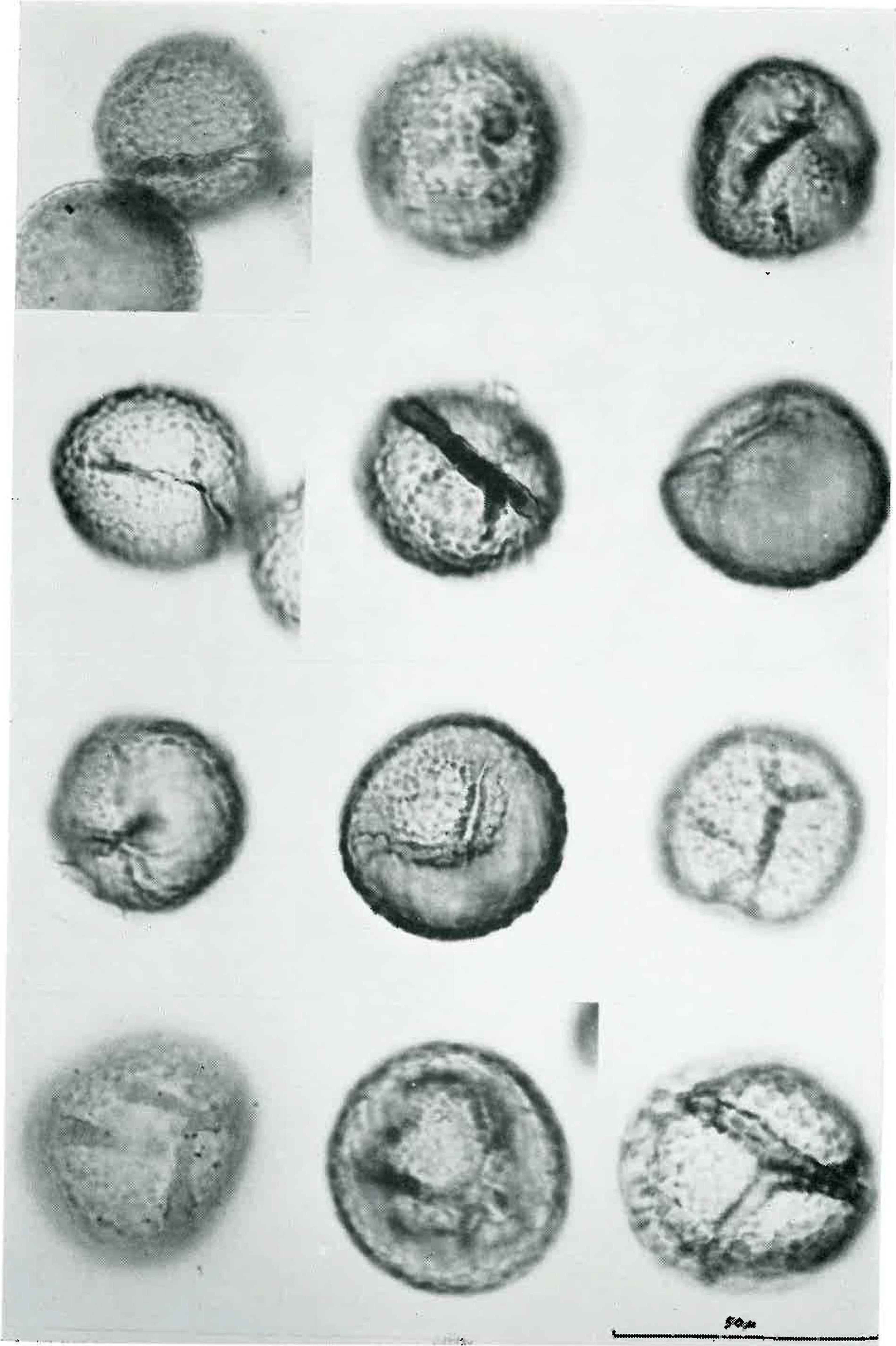


Fig. 14. Spores (legend p. 271).

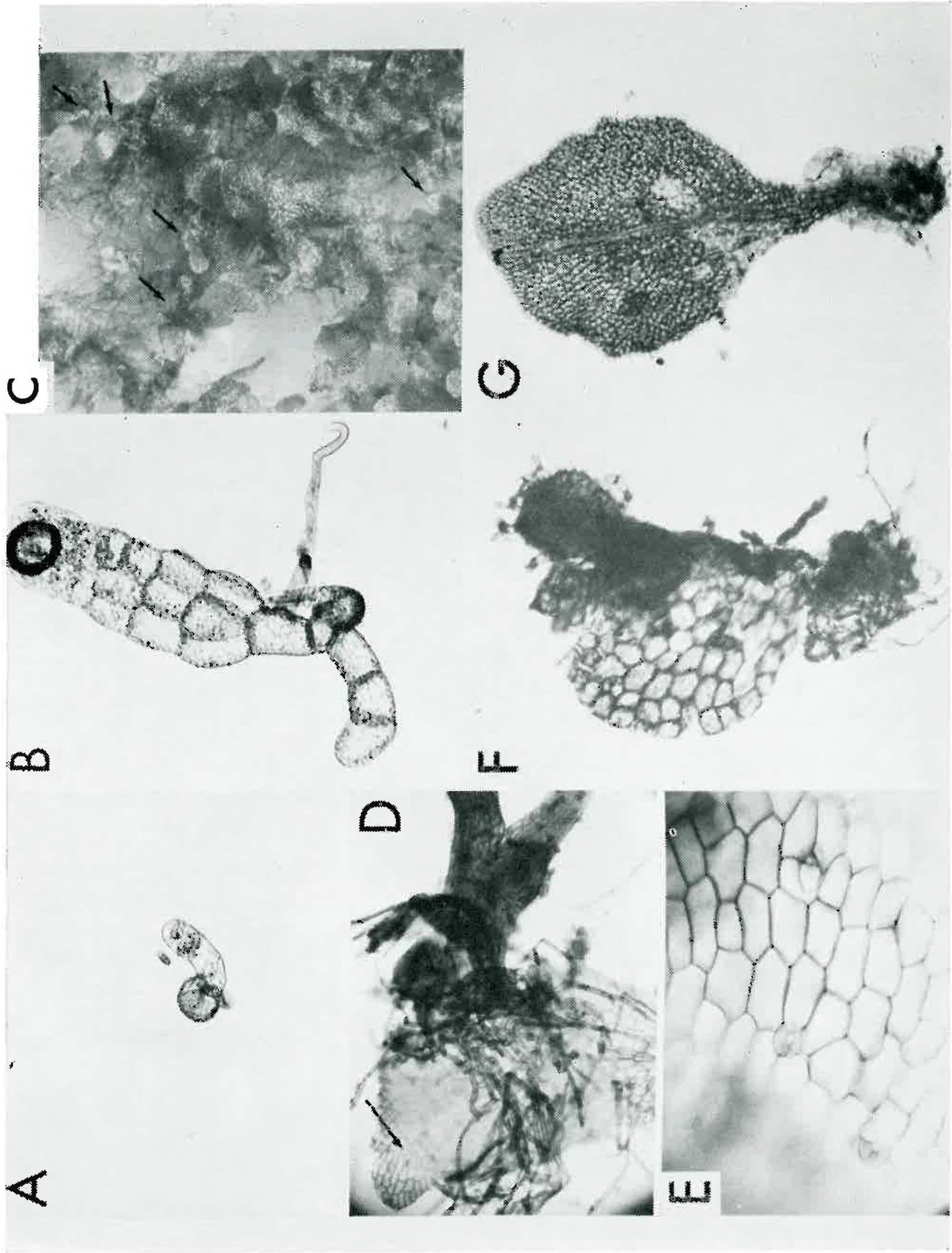


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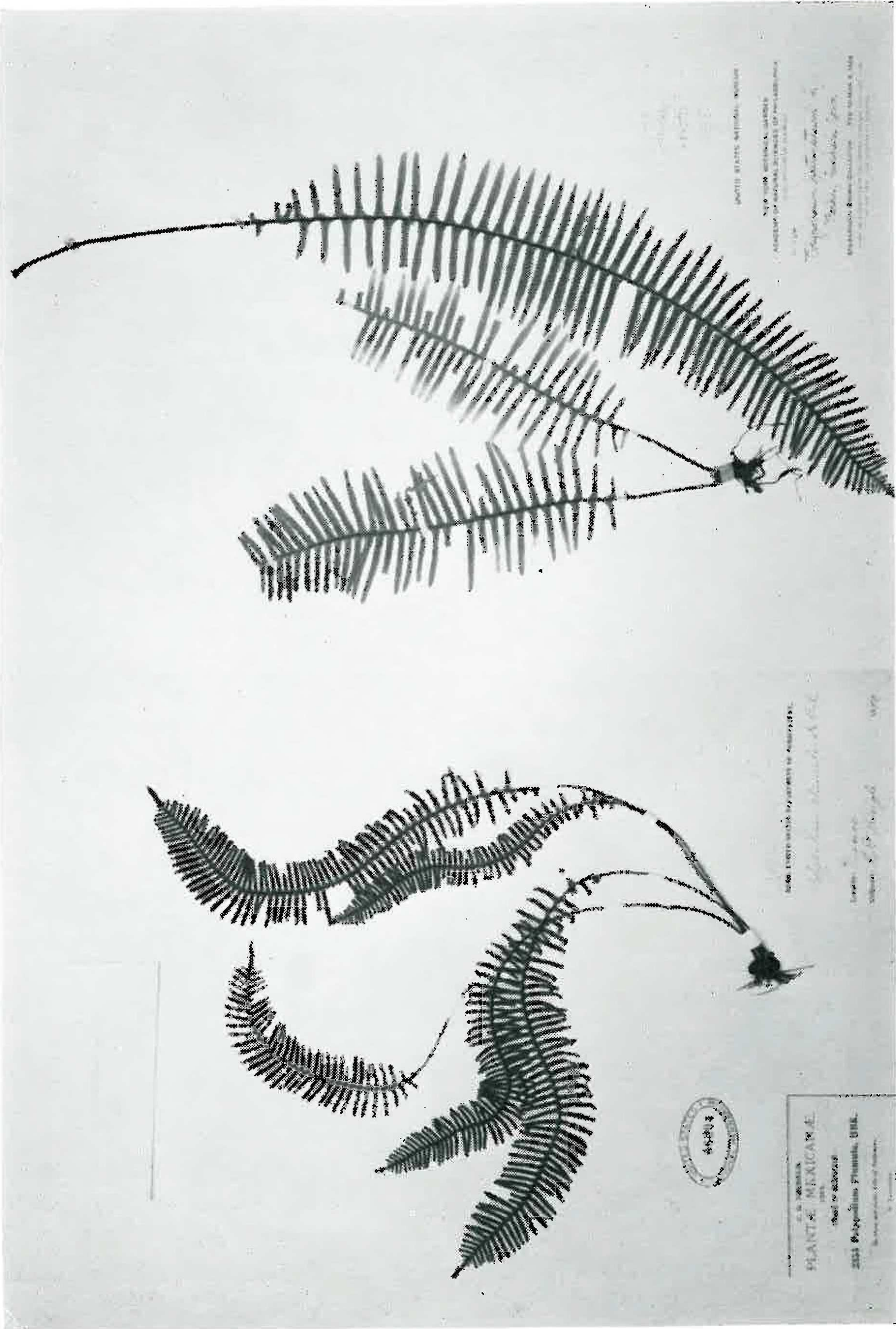


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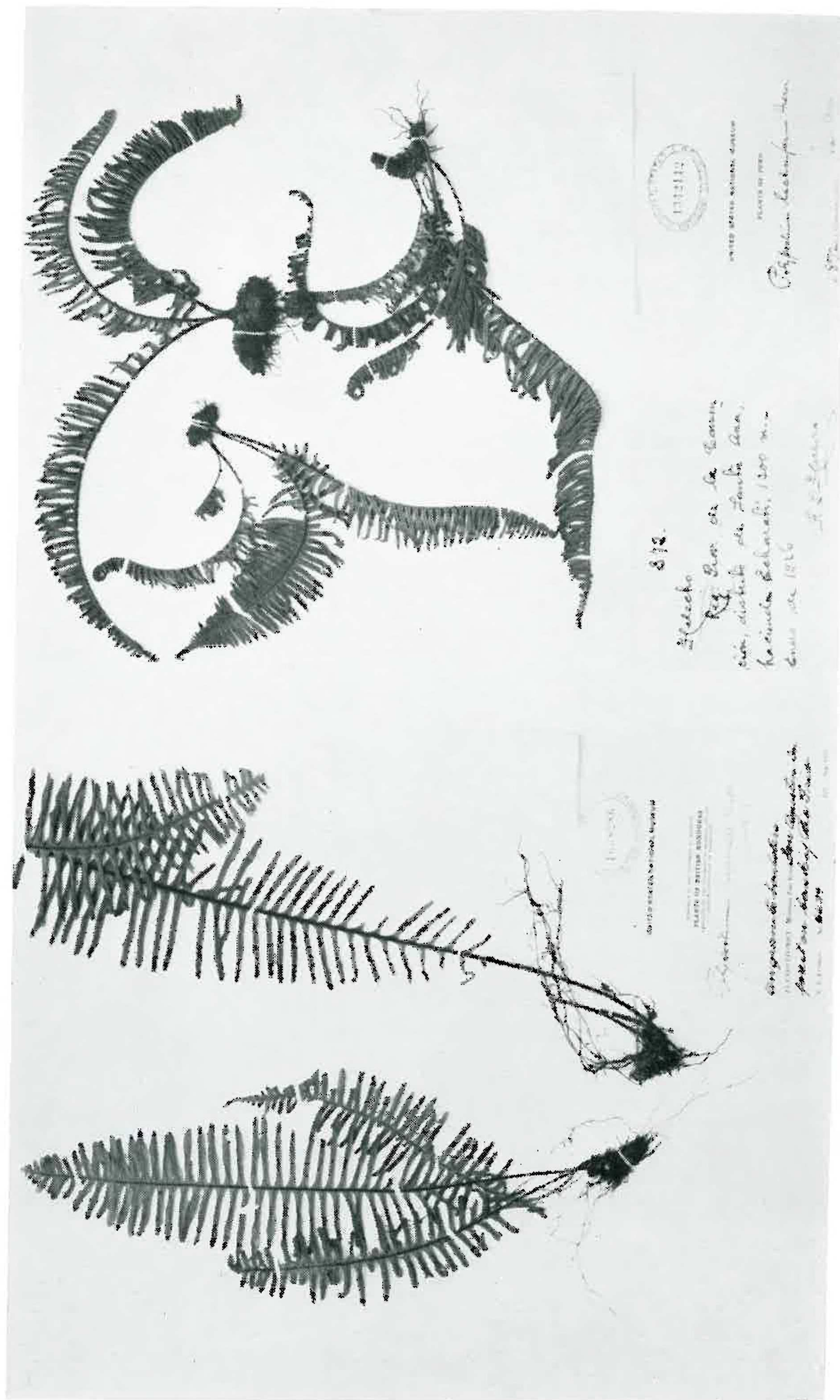


Fig. 18. Type specimens (legend p. 271).

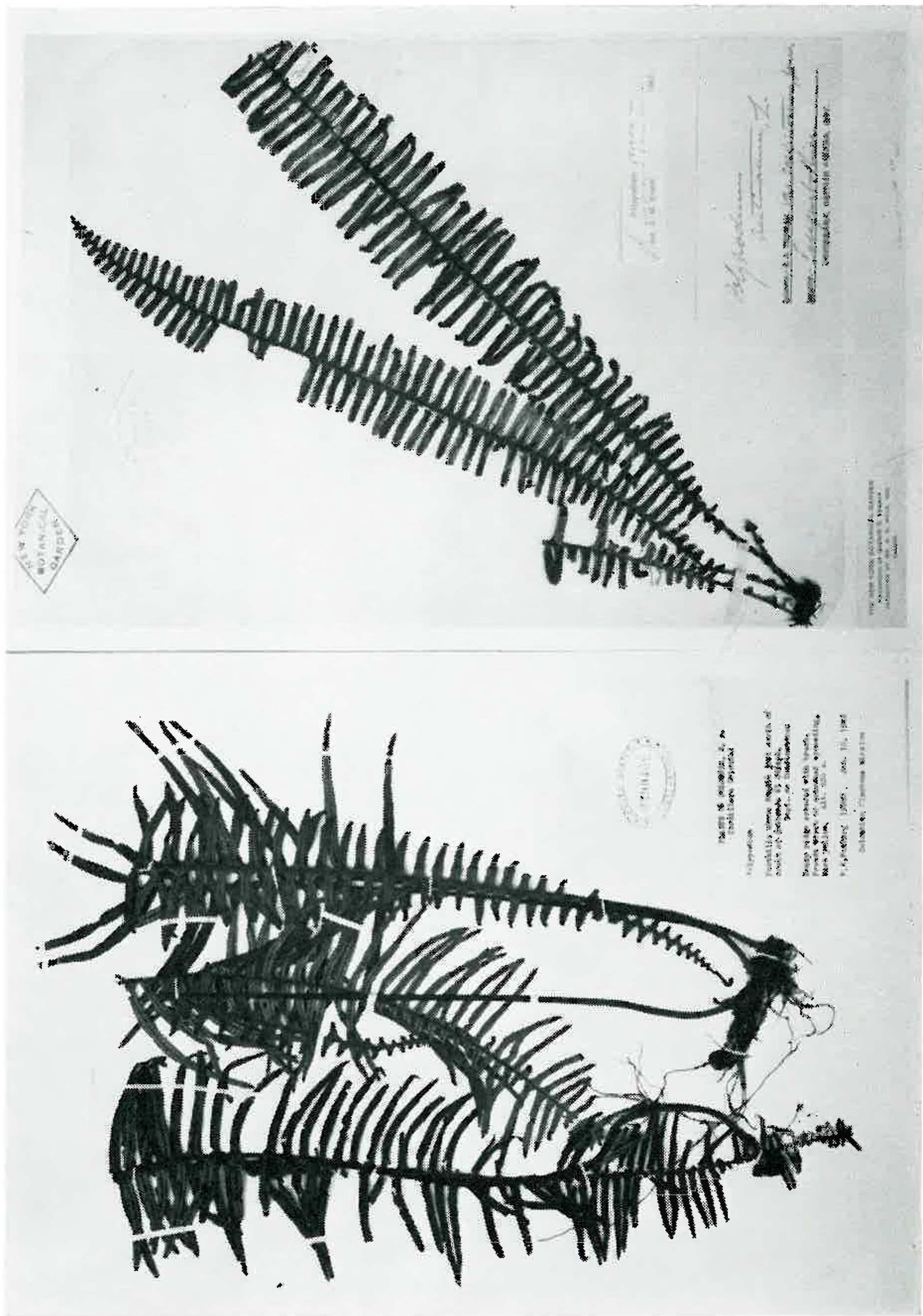


Fig. 19. Type specimens (legend p. 271).

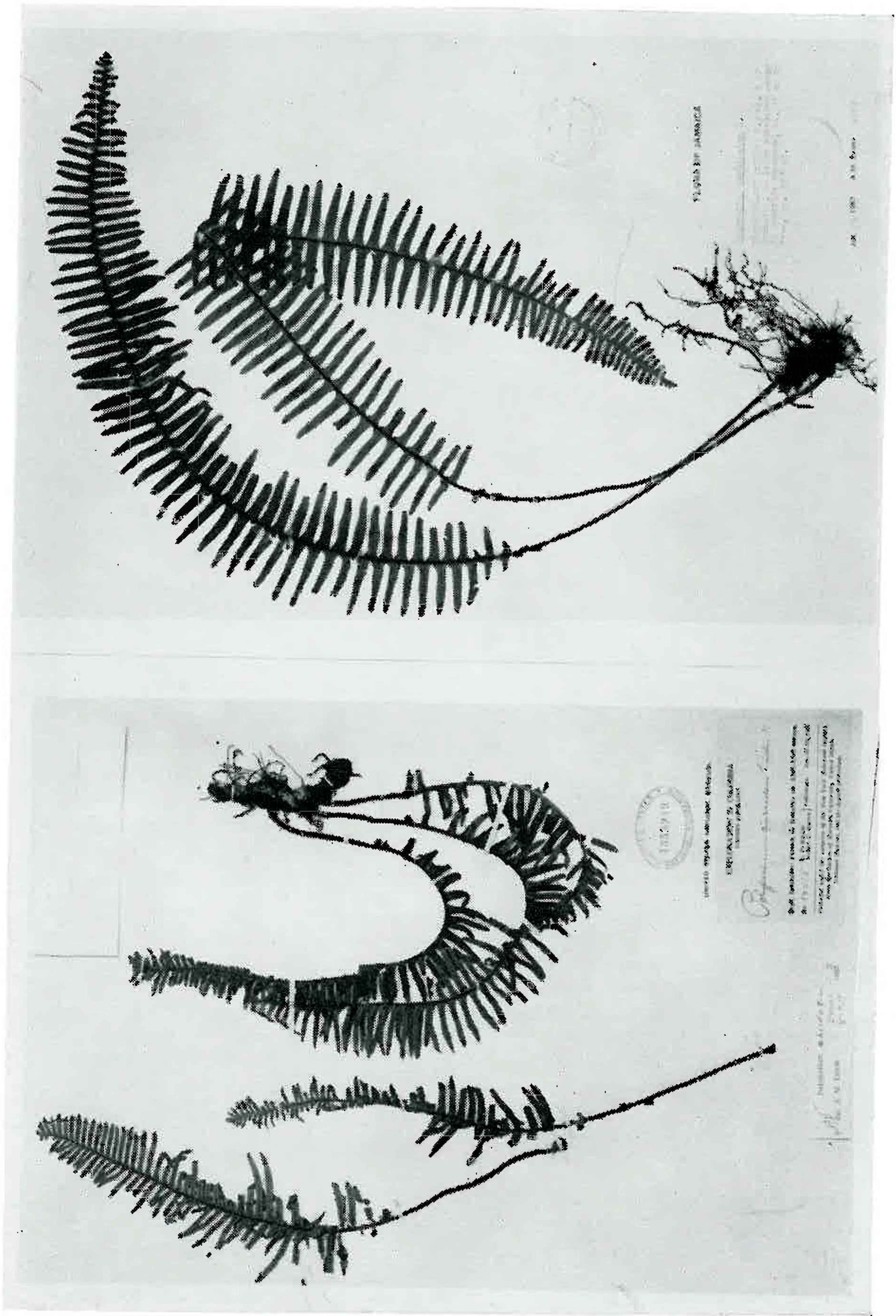


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